Physiological responses to drought of *Eucalyptus globulus* and *Eucalyptus nitens* in plantations

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Declarations

This thesis contains no material which has been accepted for a degree or diploma by the University of Tasmania or any other institution. To the best of my knowledge and belief this thesis contains no material previously published or written by another person except where due acknowledgment is made in the text of the thesis.

Donald A White

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Abstract

Eucalyptus globulus Labill. and *E. nitens* (Deane and Maiden) Maiden are the predominant hardwood plantation species in southern Australia. This thesis describes some physiological strategies exhibited by these species in response to drought as a means of determining their suitability for establishment on water limited sites. To this end a 2 ha experimental plantation was established on a low rainfall site (ca. 515 mm a^{-1}) in August 1990. The plantation was divided into irrigated and rainfed blocks so that the effects of soil drought could be separated from those of diurnal and seasonal climatic variation.

Between November 1991 and April 1993 pre-dawn leaf water potential (ψ_{max}) was significantly lower in the rainfed than the irrigated treatment for six defined periods or stress cycles. At the end of this period, when ψ_{max} was -2.37 and -2.34 MPa in the rainfed *E. globulus* and *E. nitens* respectively, leaf osmotic potential and bulk elastic modulus were still not significantly affected by water stress. At this time a significant interspecific difference was evident in the shape of the desorption isotherms. In the region of positive turgor the mean slope of these relationships was significantly greater in *E. nitens* (14.5 MPa) than *E. globulus* (9.3 MPa) resulting in turgor loss at a significantly higher relative water content in *E. nitens* (0.86) than *E. globulus* (0.79). This interspecific difference in leaf water relations was independent of soil water status.

Allometric relationships between leaf area and sapwood area were developed by destructive sampling in July 1992 and July 1993. These relationships were used with monthly growth data to plot the course of leaf area index (L*) between August 1991 and April 1993. L* was significantly lower in *E. nitens* than *E. globulus* throughout the study and was significantly reduced by water stress after November 1992. During the 1992/93 growing season the L* of the rainfed *E. globulus* increased rapidly after rewatering, resulting in a stepped pattern of leaf area development which was not observed in *E. nitens*. At the end of the

experiment, in April 1993, L* of the irrigated and rainfed treatments were, respectively, 8.3 and 6.1 in *E. globulus* and 6.9 and 4.3 in *E. nitens*.

Daily maximum stomatal conductance of both *E. globulus* and *E. nitens* was significantly reduced when ψ_{max} was <-0.55 MPa. Reduction in stomatal conductance (g_s) as ψ_{max} decreased was greater in *E. nitens* than *E. globulus*. After rewatering, stomatal conductance was slower to recover in *E. nitens* than *E. globulus*. These differences caused a significant species by water stress interaction. A phenomenological model of stomatal conductance of upper canopy foliage (g_{su}) was developed for the irrigated trees. The maximum g_{su} observed (387 mmol m^{-2} s^{-1}) was attenuated with normalised functions of total solar radiation (Q), air temperature (T) and vapour pressure deficit (D). This model explained 70% of the variation in g_{su}. The effect of water stress on the daily total of g_{su} was accommodated by predicting the ratio of total daily stomatal conductance of rainfed to that of irrigated trees as a function of the cumulative water stress integral for the preceding x days ($S_{\psi x}$), where x was eight days for *E. globulus* and 20 days for *E. nitens*. Using $S_{\psi x}$ as an independent variable accommodated the longer residual effect of water stress in *E. nitens* than *E. globulus*. The model explained 75 and 73% of the residual variation in the daily total of g_{su} of *E. nitens* and *E. globulus* after the direct effects of Q, T and D were removed.

Two estimates of canopy conductance were compared in the irrigated treatment of both species. The first (g_c) was a summation of the parallel conductances of three canopy layers and the second (g_c') involved integration of the light response function of a leaf level model with respect to cumulative leaf area index. At a daily time step g_c' explained 79% of the variation in g_c when L* was less than 6, but underestimated g_c by as much as 41% at leaf area indices above 6. This underestimation indicated that at high L*, *E. globulus* and *E. nitens* canopies may be weakly coupled to ambient atmospheric conditions. The degree of coupling was investigated in the irrigated *E. globulus* by simultaneous measurement of transpiration (using sapflow sensors) and stomatal conductance over three days in March 1994. The mean value of the dimensionless decoupling coefficient (Ω) was

0.63. Despite this, a linear relationship with D explained 85% of the variation in transpiration. The vertical profile of Ω and absorbed net radiation were examined and Ω was highest where the lowest amount of radiant energy was absorbed. It is argued that transpiration of irrigated and rainfed *E. globulus* and *E. nitens* may be calculated by treating the canopy as a single layer with a surface conductance of g_c'.

E. globulus and *E. nitens* responded to drought by stomatal closure rather than by adjustment of the osmotic or elastic properties of their leaves. This response was stronger in *E. nitens* than *E. globulus* so that on sites where water stress is moderate and seasonal, *E. globulus* will probably grow more rapidly than *E. nitens*. Another major outcome of this thesis is quantification of the different stomatal responses of the two species at the canopy scale in a way that allows transpiration to be calculated from relatively easily obtained variables. Calculation of canopy conductance as g_c' predicts a much lower value of g_s for foliage at the bottom of high L* canopies than was measured. This suggests that as L* increased the irrigated canopies of both species became more water use efficient. It is argued that if the effects of water stress on g_s and L* are considered together then long term water stress will reduce the water use efficiency of *E. nitens* more than that of *E. globulus*.

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Definition of symbols

Symbols are listed under the chapter in which they are first used.

Chapter 2		
Symbol	*Description*	*Units*
I, R	Used as abbreviations for irrigated and rainfed throughout	____
θ_s	Soil water content	mm
Δw	Soil water deficit	mm
E_t	Evapotranspiration	mm
ψ_{max}	Pre-dawn leaf water potential	MPa
u	Wind speed	m s^{-1}
h	Relative humidity	%
T	Air temperature	°C
D	Vapour pressure deficit	kPa
Q	Total solar radiation, measured in W m^{-2} at the weather station and converted to a quantum flux density for use in chapters 5, 6 and 7. The conversion factor was 1 W m^{-2} = 2.28 μmol m^{-2} s^{-1}.	μmol m^{-2} s^{-1}
R_n	Net radiation	W m^{-2}
Chapter 3		
S_ψ	Periodic or cumulative water stress integral	MPa d
ψ_{min}	Midday leaf water potential	MPa
$\Delta\psi$	Difference between pre-dawn and midday leaf water potential	MPa
W_f	Leaf fresh weight	g
ψ	Leaf water potential	MPa
W_d	Leaf dry weight	g
W_t	Leaf weight at full turgor	g
R*	Relative water content	Dimensionless
π_s	Osmotic potential at full turgor	MPa
π_p	Osmotic potential at turgor loss point	MPa
R^*_p	Relative water content at turgor loss point	Dimensionless
R^*_a	Relative apoplastic water content	Dimensionless
ε	Bulk elastic modulus	MPa
P	Turgor pressure	MPa
$\Delta\pi$	Difference between π_s and π_p	MPa
ε_{max}	Maximum bulk elastic modulus	MPa
ε_S	Bulk elastic modulus at full turgor	MPa
π	Osmotic potential	MPa

Symbols continued

Chapter 4		
A_l, A_s	Leaf and sapwood area	m^2, cm^2
l	Length of stem section	m
k_h	Hydraulic conductivity (tree basis)	
g_s	Stomatal conductance (leaf area basis)	mmol m^{-2} s^{-1}
h_t	Tree height	m
d_t	Diameter	cm
SLA	Specific leaf area	cm^2 g^{-1}
L*	Leaf area index	Dimensionless
l_u, l_m, l_l	Proportion of total leaf area in the upper, middle and lower third of the crown by depth	Dimensionless
d	days since July 1	
Chapter 5		
E	Transpiration (ground area basis)	mmol m^{-2} s^{-1}
g_a	Boundary layer conductance	mmol m^{-2} s^{-1}
c_p	Molar specific heat of dry air	J mol^{-1} °C
ρ	Density of air	mol m^{-3}
γ	Psychrometric constant	kPa °C
λ	Molar latent heat of vaporisation of water	J mol^{-1}
Δ	Slope of the relation between saturated vapor pressure and temperature	kPa °C
g_c	Canopy stomatal conductance calculated as the sum of parallel conductances of the upper, middle and lower canopy layers (equation 5.2).	mmol m^{-2} s^{-1}
g_c'	Canopy conductance calculated after Raupach (1995) with equation 5.12.	mmol m^{-2} s^{-1}
g_{su}, g_{sm}, g_{sl}	Mean stomatal conductance (leaf area basis) of the upper, middle and lower third of the canopy by depth	mmol m^{-2} s^{-1}
L^*_i	Leaf area index of the i^{th} canopy layer	Dimensionless
g_{si}	Stomatal conductance (leaf area basis) of the i^{th} canopy layer	mmol m^{-2} s^{-1}
f(Q)	Normalised g_{su} as a function of total solar radiation (Q)	dimensionless
α_g	Slope parameter of f(Q)	dimensionless
θ_g	Shape parameter of f(Q)	dimensionless
f(T)	Normalised g_{su} as a function of air temperature	dimensionless
$T_\bullet$	Temperature at which f(T) is one	°C
T_l, T_h	Low and high temperature at which f(T) falls to zero, x intercepts of f(T)	°C

Symbols continued

Chapter 5 continued		
$g_{su,i}'$	Stomatal conductance of upper canopy foliage of the irrigated trees, adjusted to remove the effects of Q and T (leaf area basis)	mmol m^{-2} s^{-1}
f(D)	Normalised $g_{su,i}'$ as a function of vapour pressure deficit (D)	dimensionless
$g_{su,max}$	Maximum stomatal conductance of the upper canopy layer	mmol m^{-2} s^{-1}
ξ	Cumulative leaf area index	dimensionless
Q_ξ	Downward flux of radiation below cumulative leaf area index of ξ	μmol m^{-2} s^{-1}
Q_0	Radiation flux incident on the top of the canopy	μmol m^{-2} s^{-1}
k	extinction coefficient	dimensionless
$g_{s,max}(\xi)$	Maximum stomatal conductance below a cumulative area index of ξ	mmol m^{-2} s^{-1}
Chapter 6.		
$g_{su,r}'$	Stomatal conductance of rainfed trees adjusted for light and temperature	mmol m^{-2} s^{-1}
t_r, t_s	Time of sunrise and sunset	hours
f(W)	Ratio of total daily conductance in the rainfed plot to total daily conductance in the irrigated plot	dimensionless
$S_{\psi x}$	Cumulative water stress integral calculated over x days	MPa d
G_c'	Daily total predicted canopy conductance, g_c'	kmol m^{-2}
G_c	Daily total calculated canopy conductance, g_c	kmol m^{-2}
Chapter 7.		
Ω	Decoupling coefficient	dimensionless
S, S_i	Mean sapflow and sapflow of the i^{th} tree (expressed on a ground area basis)	mmol m^{-2} s^{-1}
g_c	Canopy conductance (ground area basis)	mmol m^{-2} s^{-1}
g_{sc}	Surface conductance (ground area basis)	mmol m^{-2} s^{-1}
g_a	Boundary layer conductance (ground area basis)	mmol m^{-2} s^{-1}
g_c'	Canopy conductance calculated with equation 7.3	mmol m^{-2} s^{-1}
g_{sc}'	Surface conductance calculated with equation 7.4 using g_c' (ground area basis)	mmol m^{-2} s^{-1}

Symbols continued

Chapter 7 continued		
g_a'	Boundary layer conductance calculated with equation 7.5 using g_c' and g_{sc}' (ground area basis)	mmol m^{-2} s^{-1}
Ω'	Decoupling coefficient calculated with equation 7.6 using g_a' and g_c' (ground area basis)	Dimensionless
P	Atmospheric pressure	kPa
D_s	VPD at leaf surface	kPa
β	emissivity	dimensionless
C_p	Molar specific heat of dry air	J mol^{-1} $°C^{-1}$
E_m	Transpiration calculated after Meinzer et al. (1993) using equation 7.8, assumes Ω=0.	mmol m^{-2} s^{-1}
E_{imp}	Transpiration calculated after Tan and Black (1976) using equation 7.9, assumes Ω=0	mmol m^{-2} s^{-1}
E_{eq}	Transpiration calculated using equation 7.10 after McNaughton and Jarvis (1983), assumes Ω=1	mmol m^{-2} s^{-1}
E_Ω	Transpiration calculated by partitioning between E_{imp} and E_{eq} using Ω using equation 7.11 after McNaughton and Jarvis (1983).	mmol m^{-2} s^{-1}

Chapter 1. Introduction

1.1 The problem

The hardwood plantation estate in Australia is 0.12 Mha and current plantings exceed 13 kha a^{-1} (Australian Bureau of Agricultural and Resource Economics 1994). Most of these plantings are in SE and SW Australia to two fast-growing species, *Eucalyptus globulus* Labill. and *E. nitens* (Deane and Maiden) Maiden. In SW Australia, *E. globulus* is already planted on sites where available water limits growth and drought deaths were observed during a dry summer in 1993/94 (Dutkowski 1995). Further expansion of the plantation estate in SE Australia will almost certainly necessitate establishment on water limited sites. An understanding of the physiological strategies exhibited by *E. globulus* and *E. nitens* in response to water stress, and the impact of these strategies on the relationship between growth and water use, is desirable for determining their suitability for short rotation forestry and site selection for these species.

1.2 Background

Available water has often been described as the most significant factor limiting plant growth on a global basis (eg. Bewlay and Krochko 1982, Blake and Tschaplinski 1992). Despite this, consistent relationships amongst plant water status, growth and water use have proved elusive (Slatyer 1957, Turner 1986, Munns 1988), largely because water stress affects plant growth and water relations at all scales from the molecular to the whole tree and beyond.

The inter-relationships between growth and water use will differ between natural and managed ecosystems. Moreover, in managed forests the objectives of management will determine the most desirable inter-relationship. In natural forests interspecific competition is important and species may develop mechanisms that allow them to be competitive over a narrow range of environmental conditions. In such systems growth rate may or may not influence survival under water limited

conditions. In managed monocultures wood production and the efficiency with which harvestable biomass is produced become important. In plantations managed for wood production the impact of forest management practices on catchment water yield is increasingly recognised as an important indicator of the sustainability of forestry at a regional scale (Calder 1986, Dye 1987).

Several general mechanisms of drought resistance have been described (eg. Levitt 1972, Jones, M.M. et al. 1981, Jones, H.G. 1992). Since there are costs associated with mechanisms of drought resistance they will usually reduce yield (Jones, H.G. 1992, 1993, Table 1.1). It has become common to adopt water use efficiency as a criterion for selecting planting stock (Jones, H.G. 1993). This is an appropriate strategy where water is either a major component of the systems cost structure or stream flow is an important output from the catchment (Calder 1986, Dye 1987, Roberts and Rosier 1993). Unfortunately most drought response strategies will reduce water use efficiency at the canopy scale (Jones, H.G. 1993), making it an inappropriate criterion to use when selecting plant material for wood production on water limited sites. This line of logic leads to the rather counter-intuitive conclusion that plants which do not respond to drought will grow fastest during drought. Unfortunately they will only continue to do so while they survive. This trade off between growth and survival is the crux of species selection for water limited sites.

Table 1.1 Drought-tolerance mechanisms (Jones, H.G. 1992)

Tolerance Mechanism	Cost
1. Avoidance of plant water deficit	
(a) Drought escape - short growth cycle, dormant period	Short season
(b) Water conservation - small leaves, limited leaf area, stomatal closure, low cuticular conductance, low light absorption	Available water not used
(c) Maximal water uptake - good root system	Structural costs
2. Tolerance of plant water deficits	
(a) Turgor maintenance - osmotic adjustment, low elastic modulus	Metabolic costs
(b) Protective solutes, desiccation-tolerant enzymes, etc.	Metabolic costs
3. Efficiency mechanisms	
(a) Efficient use of available water	Low maximum rate of growth and water use
(b) Maximal harvest index	?

1.3 Objectives and a hypothesis

1.3.1 Plantation production, objectives

Growth will be limited by available water where it is insufficient to meet evaporative demand. For fast growing *Eucalyptus* plantations this is expected to occur wherever potential evaporation exceeds rainfall, unless there is access to stored ground water.

Such water limitation might affect plantation yield in three ways:

- By reducing carbon assimilation per unit leaf area. There is evidence to suggest that, during moderate water stress, this limitation occurs principally in the gaseous phase (ie. due to stomatal closure rather than to reduced photosynthetic capacity). There is also evidence that stomatal closure due to drought stress may result in photoinhibition at high irradiance (Cornic 1994, Ögren 1994).
- By reducing leaf area development during the growing season.
- By reducing the proportion of carbon allocated to stem wood (Waring et al. 1980)

In addition drought might increase the amount of water transpired per unit of carbon assimilated (ie. water use efficiency will be reduced) (Jones, H.G. 1993).

With these probable impacts of drought in mind this thesis addresses two questions:

I. What physiological strategies are adopted by *E. globulus* and *E. nitens* in response to repeated cycles of moderate drought stress?[1]

II. How do the strategies adopted by these species affect relationships between growth and water use?

[1] For the purposes of this thesis moderate drought stress is defined by predawn water potentials between -0.55 and -2.5 MPa.

The implications for plantation establishment on water limited sites of answers to questions I and II are discussed in the concluding chapter?

1.3.2 Ecological implications, a hypothesis

Ecological studies consider the distribution of species in relation to a range of atmospheric and edaphic factors. In asking which of these two plantation species is better suited to water limited sites the main context is wood production. If *E. globulus* and *E. nitens* are to be the focus of future plantation establishment programs it might also be instructive to consider their natural distributions as a means of generating a hypothesis as to their likely performance on drought prone sites.

E. globulus and *E. nitens* both belong to the subgenus Symphyomyrtus, series *Viminales* and subseries *Globulinae* (Pryor and Johnson 1971). While they are taxonomically similar their distributions do not overlap. *E. nitens* occurs between 850 and 1200 m above sea level, where it is regularly subjected to freezing temperatures (Pederick 1979). Most *E. nitens* plantations in south eastern Australia are descended from populations of juvenile persistent *E. nitens* in the Victorian central highlands, collectively known as the Western provenance (Pederick 1979). In contrast *E. globulus* is found at low altitude (usually <300 m, Kirkpatrick 1974, 1975) and over a wide range of rainfall. Consistent with these distributions, in plantations in southern Tasmania *E. nitens* hardened in winter to lower temperatures than *E. globulus* (Hallam et al. 1989). This was probably the result of differences in solute accumulation in the foliage. This thesis tests the hypothesis that traits which confer cold tolerance on *E. nitens* will also render it more drought tolerant than *E. globulus*.

1.3.3 Isolating soil moisture effects

Defining physiological responses to drought (objective I, section 1.3.1) requires that the effect of soil water deficit be isolated from seasonal and diurnal rhythms in response variables. The most effective way to do this is to compare the behaviour of water limited trees with that of well-watered controls so that the real effect of

soil water deficit may be quantified. While this is a fundamental tenet of experimental design which has been routinely applied in experiments with seedlings, due to logistical problems it has not been universally practiced in investigations of the effect of soil moisture deficit on larger trees. A common approach, particularly in ecological studies, has been to measure the same trees throughout a period of water stress and interpret changes in leaf water relations variables (Parker et al. 1982) and gas exchange characteristics (Sinclair 1980, Carbon et al. 1981, Attiwill and Clayton-Greene 1984) as responses to water stress. The experiment on which this thesis is based incorporated a replicated irrigated control. Results presented in chapter 3, 5 and 6 highlight the importance of such controls for interpreting variation in osmotic potential and stomatal conductance.

1.4 Summary

The thesis is divided into eight chapters. This first is a general introduction. The contents of the remaining chapters are briefly described below.

Chapter 2. Experimental design, establishment and maintenance

This chapter describes the design, establishment, management, maintenance and measurement of the 2 ha field experiment at which all the research was done.

Chapter 3. Leaf water relations

Pre-dawn water potential is reported along with leaf water relations variables, including osmotic potential at full and zero turgor, relative water content at incipient plasmolysis, relative apoplastic water content and bulk leaf elastic modulus. This chapter has been published, in a slightly different form, in Tree Physiology as:

White, D.A., Beadle, C.L. and Worledge, D (1996). Leaf water relations of *Eucalyptus globulus* ssp. *globulus* and *E. nitens*: seasonal, drought and species effects. *Tree Physiol.* 16: 469-476.

Chapter 4. Leaf area development and leaf area to sapwood area ratios

The course of leaf area development is plotted for the irrigated and rainfed treatment of both species. Leaf area index is calculated using linear relationships between leaf area and sapwood area with monthly growth data collected in the plantation. The effect of water stress and species on the slope of these linear relations is also discussed.

Chapter 5. Leaf and canopy stomatal conductance under irrigated conditions

A phenomenological model is developed to predict the stomatal conductance of upper canopy foliage in the irrigated treatment of *E. globulus* and *E. nitens*. Two estimates of canopy conductance are compared.

Chapter 6. The effect of water stress on stomatal conductance

Stomatal conductance measurements made during the growing seasons of 1991/92 and 1992/93 are analysed to test for the effects of canopy position, species, water stress and species by water stress interactions. The results of these analyses are used as a basis for incorporating the effect of water stress in the phenomenological model developed in chapter 5.

Chapter 7. Control of transpiration in irrigated *E. globulus*

Simultaneous measurements of transpiration and stomatal conductance in irrigated *E. globulus* are described and used to make an indirect calculation of the dimensionless decoupling coefficient (Ω, McNaughton and Jarvis 1983). A second experiment examines the vertical profile of Ω within the same canopy. The results are used to decide whether single or multiple layer models are more appropriate for calculation of transpiration.

Chapter 8. General summary

All of the results presented in the preceding 5 chapters are summarised and considered in the context of the questions asked and hypotheses advanced in the first chapter.

Chapter 2. Design, establishment and management of an experimental plantation

2.1 Introduction

In August 1990 a 2 ha plantation was established approximately 30 km east of Hobart (Figure 2.1), to address the questions and hypothesis advanced in Chapter 1. Unless otherwise stated data reported were measured in this plantation. This Chapter describes the site, experimental design, plant material, treatments and establishment and management protocols applied.

2.2 Site description

The experiment was established on an ex-pasture site in a low rainfall zone (*ca.* 515 mm a^{-1}) of south-east Tasmania (Prosser 8412: Lat. 42°49' S, Long. 147°36' E, Figure 2.1). The aspect is westerly and the average slope 5°. The soil has a shallow red-brown loam A horizon and a light brown medium clay B horizon occasionally overlying light yellow-brown gritty loam from decomposing rock (type: chocolate soil, Stace et al. 1968). The parent material is basalt though sandstone floaters occur in the south-western corner of the plantation. Mean soil depth to bedrock or rock floaters is 0.6m.

2.3 Plantation establishment

Prior to planting, 26 rows were ripped at 3.5 m intervals to a depth of 0.5 m and a 1m wide strip, 0.5 m either side of the rip line, was sprayed with atrazine (6 kg ha^{-1}) and glyphosate (1.5 kg ha^{-1}) for residual and knockdown weed control respectively. The herbicides were diluted in 260 litres of water with 0.1% Pulse and 2% Liase added as surfactant and anti-antagonist respectively. An electrified, rabbit-proof fence was erected to exclude large herbivores.

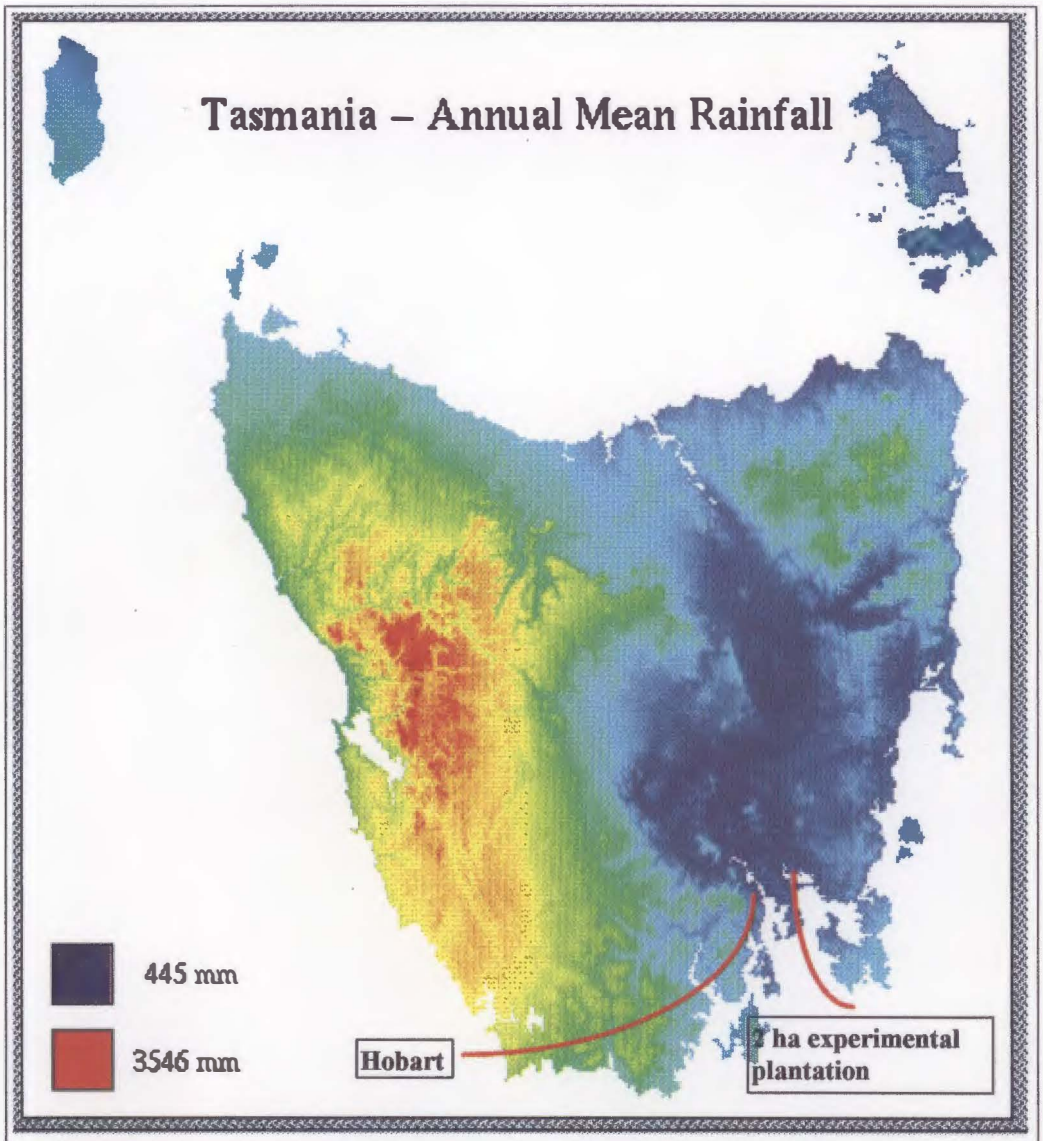

Figure 2.1 A map of Tasmania showing the locality of the experimental plantation. The map is coloured so that the blue and red ends of the spectrum indicate low and high rainfall respectively.

2.4 Experimental design

2.4.1 Plant material and layout

Seedlings of two seedlots each of *E. globulus* and *E. nitens* (Table 2.1) were planted at 2 m intervals in the rip-lines in August 1990 to give a stocking of 1430 stems ha^{-1}.

The plantation was divided into six blocks. Three blocks each were designated as irrigated (I) and rainfed (R). Each block was 26 rows by 19 trees and included four subplots: 11 rows of the King Island provenance of *E. globulus* and improved second generation 'Western provenance' of *E. nitens* together with 3 rows of the Barrington Tops provenance of *E. nitens* (Pederick 1979) and a single row of the Rheban provenance of *E. globulus* (Table 2.1). Within each block the position of these four seedlots was allocated at random (Figure 2.2). All seedlots were included in measurements of growth (24 subplots) but only the King Island provenance of *E. globulus* and the improved seedlot of *E. nitens* (Table 2.1) were included in measurement of water use (12 subplots) and physiological variables.

Growth plots. In each subplot a growth plot was established. In the major seedlot (King Island *E. globulus* and 'Western provenance' *E. nitens*) of each species the growth plots were 5 rows of 6 trees while in the other seedlots they were a single row of 15 trees (Figure 2.2).

Physiology plots. In one replicate of the irrigated (I) and rainfed (R) treatments of each species a nine-tree plot (3 x 3) was established in which physiological measurements were made (Figure 2.2). All physiological data except those reported in Chapter 7 (Figure 2.2) were collected in these four plots.

← North

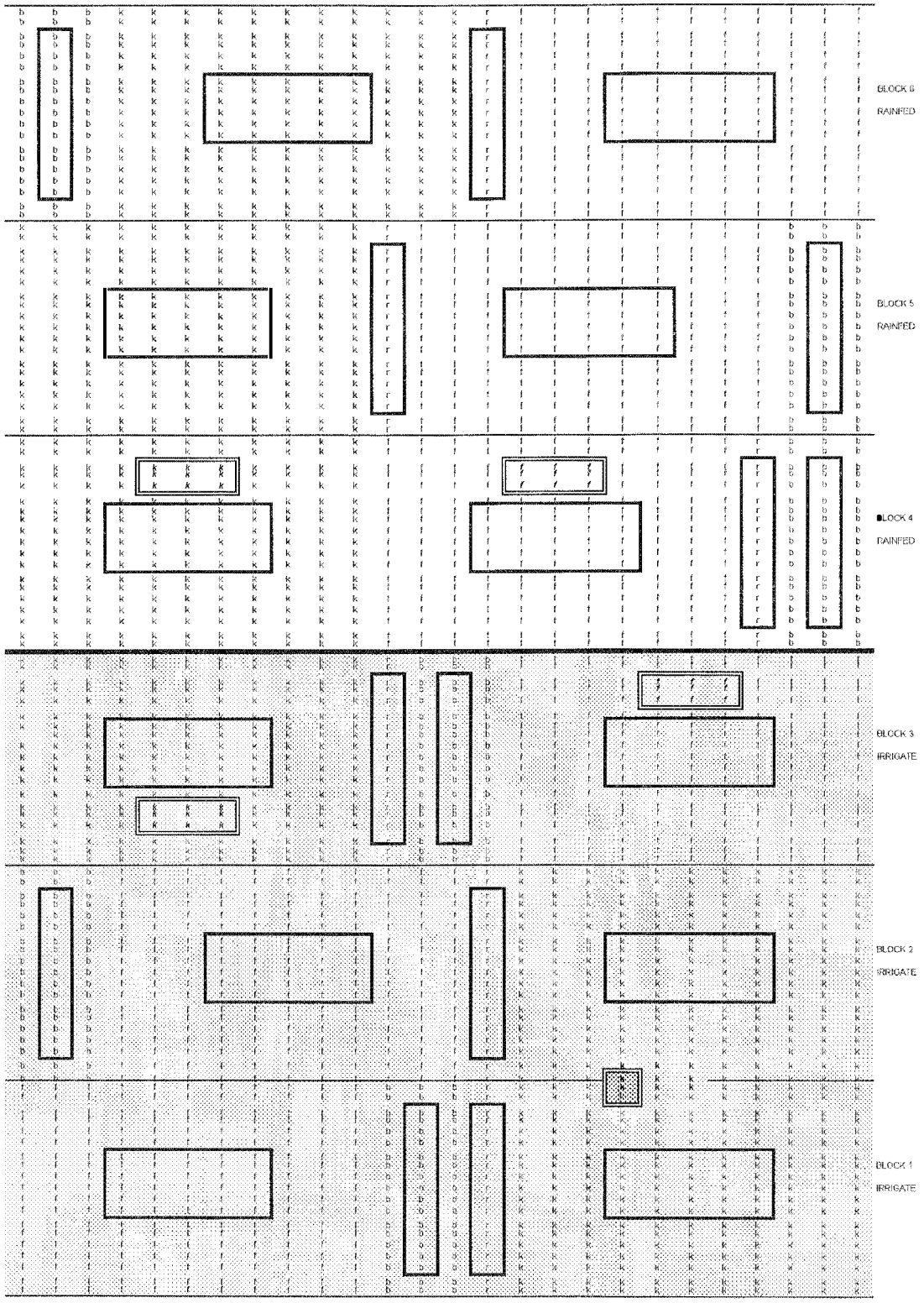

Figure 2.2 Layout of the experimental plantation. Each letter represents a tree where k=King Island *E. globulus*, r=Rheban *E. globulus*, f=Forest Resources seed orchard *E. nitens* and b=Barrington Tops *E. nitens* (Table 2.1). The six blocks are labelled and separated by fine lines, growth plots are delineated by a thick line and physiology plots by a double line as are a group of three trees used in two experiments described in chapter 7.

Table 2.1. List of seedlots planted.

Species	Seedlot	Latitude (S)	Elevation (m)	Rainfall
E. globulus	King Island	39°55'	50	990
E. globulus	Rheban (CSIRO S16589)	42°42'	120	575
E. nitens	Forest Resources Seed Orchard	37°50'	>850	—
E. nitens	Barrington Tops (S16304)	32°00'	1500	Not known

2.4.2 Soil water measurements

Soil water data were used with pan evaporation to schedule irrigation in the irrigated control blocks and as an indicator of water stress in the rainfed blocks. The data belong to Mr JL Honeysett and Mr D Worledge and will appear in subsequent publications on hydrological aspects of the experiment. For completeness, their measurement protocol is described below.

Four access tubes for measurement with a neutron moisture meter (NMM, CPN503, Pacheco, California) were installed within each of the 12 growth plots. The tubes were placed immediately opposite the midpoint between a randomly selected pair of trees, the first two at 0.5 m and 1.0 m, and the other two at 1.75 m from the rip-line. The first two and one of the latter were advanced to full soil depth by auguring inside the tube to bedrock. Depth varied from 0.5 to 1.0 m. The fourth tube was placed in an oversized hole mechanically drilled into the rock base to a total depth of 3.0 m and set in a slurry of kaolin and cement (Prebble et al. 1981). Separate calibrations were obtained from field sampling for the surface (0-0.125m) and subsurface (0.125-1.0m) for both the normal and cemented tubes. Soil water content (θ_s) was measured at 0.15 m intervals down to 1.0 m and 0.3m intervals thereafter. θ_s was calculated as total soil water content (mm) in zone 1 (0-1.0m) and zone 2 (1.0-3.0m) for each of the twelve plots. Soil water deficit (Δw) and evapotranspiration (E_t = total water use including canopy interception) were calculated using a soil water balance equation (Honeysett et al. 1992). Measurements were generally made every two weeks from October to March and less frequently at other times.

2.4.3 Irrigation system

In October 1991 an automatic watering system was installed in the three blocks designated as irrigated. The irrigated area was divided into 4 zones of 0.25 ha each with an automatic timer controlling a solenoid valve in each zone. Water was delivered across the middle of the plantation through 50 mm poly-pipe and 19 mm laterals laid from this up and down each inter-row (25 in all). Microsprinklers were positioned every 4 m along these laterals to provide an overlap of 50%. The sprinklers were designed to compensate for pressure increases from the top to the bottom of the irrigated area and deliver 5 mm per hour. Only one zone could be watered at a time. Irrigation was usually scheduled at night to minimise evaporative losses and maximise infiltration.

2.4.4 Treatments

Irrigated. Irrigation of the irrigated (I) blocks was scheduled to maintain soil water deficit (Δw) between 20 and 40 mm. Experience at other sites suggested that in this range adequate root development was encouraged without water availability being limiting for growth.

Rainfed. Trees in the rainfed (R) replicates were subjected to stress cycles that were separated by rainfall or supplementary irrigation. Details of these cycles are given in Chapter 3.

2.5 Plantation management

2.5.1 Fertiliser application

Phosphorus was applied at planting as triple super phosphate at 120 kg ha^{-1} elemental P. In 1990/91 and 1991/92, nitrogen was applied as urea at 100 kg ha^{-1} elemental N (40% in August, 30% in both December and March). Due to the presence of some stem deformities at the end of the second year of growth (Turnbull et al. 1994), only 60 kg ha^{-1} N was applied in August 1992 and 1993.

2.5.2 Weed control

Post planting weed control was limited to the 1 m intra-row strip in 1990/91 to minimise instability and unacceptable soil loss. Control was maintained in this period by hand hoeing and application of glyphosate using hand-held wick-wipers (2:1 water: glyphosate with 0.1% Pulse). The inter-row was slashed periodically to prevent shading of trees by long grass. Subsequent control of the inter and intra-row was by shielded spraying using the same mixture as for the pre-planting spray with substitution of simazine for atrazine. Single applications were applied in the second and third years of growth only.

2.5.3 Insect control

Insect control was undertaken each winter for autumn gum moth (*Mnesampela privata*). Juvenile foliage of both species was attacked although loss of canopy was more severe in *E. nitens*. Juvenile foliage of *E. globulus* was also attacked by bluegum psyllids (*Ctenarytaina eucalypti)* which impair apical growth. The trees were sprayed with a mixture of Nuvacron 400 (0.5 l ha^{-1}) and Dominex (0.25 l ha^{-1}). Nuvacron and Dominex were also used to control sawfly larvae in January 1992.

2.6 Measurement program

2.6.1 Indicators of water stress

Two primary indicators of soil and plant water deficit were used: soil water deficit (Δw) calculated from fortnightly neutron moisture meter data (after Honeysett et al. 1992) and pre-dawn leaf water potential (ψ_{max}) measured for all the trees in the physiology plots using a pressure chamber (Scholander et al. 1965). ψ_{max} was measured as often as weekly. The frequency of measurement depended on how quickly ψ_{max} was changing.

2.6.2 Climate

In September 1991 a manual weather station was established approximately 750 m from the plantation. Wet and dry bulb, maximum and minimum thermometers and a

thermohygrograph were mounted in a Stephenson screen. Located nearby were a manual rain gauge, wind run anemometer and class A evaporimeter pan. Wind run and pan evaporation were recorded at least twice weekly. Wet and dry bulb temperature, weekly maximum and minimum temperature were recorded at 0900 h every Friday.

In March 1992 an automatic weather station was established adjacent to the manual station. Wind speed (u) was measured with a cup anemometer and rainfall by a tipping-bucket rain gauge with a 0.2 mm bucket. Relative humidity (h), air temperature (T) and vapour pressure deficit (D) were measured with a screened Vaisala probe and total solar radiation (Q) with a Li-Cor LI-200s pyranometer. All of the above instruments were mounted 6 m above ground on a tower. Net radiation (R_n) was measured with a Fritschen-type net radiometer mounted above the subject trees. All of u, h, T, D, Q, and R_n were sensed every 5 minutes and the average recorded hourly. Prior to March 1992 Q and D were obtained from the Bureau of Meteorology weather station at the Hobart Airport, approximately 10 km from the experiment site.

2.6.3 Plant responses

A range of plant response to soil water deficit (indicated by Δw and ψ_{max}) and diurnal variation in u, h, T, D, Q and R_n are introduced and described in subsequent chapters.

Chapter 3. Leaf water relations

3.1 Introduction

Of the drought tolerance mechanisms listed in Table 1.1, those which sustain turgor are most likely to maximise growth rates under moderate drought. Changes in turgor pressure provide a crucial link between changes in plant water status and many growth-related processes which are influenced by water deficit (Hsiao et al. 1976, Bradford and Hsiao 1982, McDonald and Stadenberg 1993). Turgor maintenance can be achieved through changes in osmotic potential and/or tissue elasticity (Tyree and Jarvis 1982). A decrease in osmotic potential results in greater turgor pressure at a given leaf water potential while an increase in cell wall elasticity results in smaller changes in turgor pressure for a given change in relative water content. The capacity of a range of plant species, including eucalypts, to regulate osmotic potential (Clayton-Greene 1983, Bowman and Roberts 1985a, b, Myers and Neales 1986, Abrams 1990) and cell wall elasticity (Cheung et al. 1975, Melkonian et al. 1982, Robichaux et al. 1983, Bowman and Roberts 1985b) in response to drought has been demonstrated.

The natural distribution of *E. nitens* is at high altitude (>850 m asl) where it is regularly subjected to freezing temperatures (Pederick 1979) whereas *E. globulus* is found at low altitude (usually <300 m asl, Kirkpatrick 1974, 1975). In plantations in southern Tasmania *E. nitens* hardened in winter to lower temperatures than *E. globulus* (Hallam et al. 1989). In this chapter the null hypothesis tested is that the greater cold tolerance of *E. nitens* compared to *E. globulus* (Hallam et al. 1989) will also render it more drought tolerant than *E. globulus* and more able to respond to drought stress by adjustments in its tissue water relations. Osmotic and elastic properties of both species were investigated by pressure-volume analysis (Scholander et al. 1964, Tyree and Hammel 1972) over a two-year period which included six drought cycles. The irrigated control plots were used to separate the effects of drought from those caused by seasonal changes at the experimental site.

3.2 Materials and Methods

3.2.1 Soil and plant water status

At frequent intervals throughout the experiment, single leaves were excised from each of the nine trees of the irrigated (I) and rainfed (R) physiology plots (Figure 2.2) of both species to estimate pre-dawn water potential (ψ_{max}). For the periods between each measurement of ψ_{max} a water stress integral (S_ψ) using a baseline of 0.2 MPa. S_ψ was calculated after Myers (1988) as the sum of daily absolute values of ψ_{max} (less the baseline value) for a given period. Values for ψ_{max} between measurement times were calculated by linear interpolation.

Three trees were randomly selected from within each of the four physiology plots (I and R, x 2 species). On 10 occasions between July 27, 1991, and February 27, 1992, midday leaf water potential (ψ_{min}) of these trees was measured and the difference between ψ_{max} and ψ_{min} ($\Delta\psi$) calculated as an estimate of the daily maximum gradient of leaf water potential from root to leaf.

3.2.2 Sampling and rehydration

The same 12 trees on which ψ_{min} was measured were used for examination of leaf water relations. On nine occasions between September 1991 and April 1993, a single leaf was excised from each of these twelve trees for pressure-volume (p-v) analysis (Tyree and Hammel 1972). Leaves were excised under de-ionised water and rehydrated in airtight containers in the dark for between three and four hours. Turner (1987) suggested that 3-4 hours was sufficient for woody species to achieve full turgor without further uptake of water into intercellular spaces (Parker and Pallardy 1987). Only the youngest fully expanded leaves from the top third of the crown were selected. Up to and including the sampling in May 1992 only juvenile leaves were used. Thereafter adult leaves were used.

3.2.3 Measurement and derivation of tissue water relations parameters

Pressure-volume (p-v) curves were constructed by allowing leaves to dry on a laboratory bench while periodically measuring fresh weight (W_f) and water potential (ψ). Leaves were weighed before (W_1) and after (W_2) ψ was measured. Fresh weight was calculated as the average of W_1 and W_2. After measurement, leaves were dried to constant weight at 80°C (W_d). Turgid weight (W_t) was estimated from a plot of ψ versus W_f by extrapolation to $\psi = 0$ (Davie et al. 1993). Relative water content (R*) was calculated as:

$$R^* = \frac{(W_f - W_d)}{(W_t - W_d)} \tag{3.1}$$

3.2.4 Estimation of tissue water relations variables

Osmotic potential at full turgor (π_s) and turgor loss point (π_p), relative water content at turgor loss point (R^*_p) and relative apoplastic water content (R^*_a) were derived from the p-v curves (Tyree and Hammel 1972, Turner 1987). Bulk elastic modulus (ε) was calculated after Bowman and Roberts (1985b) as:

$$\varepsilon = \frac{\Delta P}{\Delta R}(R^*_x - R^*_a) \tag{3.2}$$

where R^*_x was the mean R* over the calculation interval, ΔR^*, and ΔP was the change in turgor pressure over the same interval.

Results were analysed as a factorial with respect to treatment (I and R) and species. Separate analyses were conducted for $\Delta\psi$, π_s, π_p, $\Delta\pi$, ε_{max}, ε_s, W_d/W_t, R^*_p and R^*_a for each measurement time. $\Delta\pi$ is the difference between π_s and π_p, ε_{max} and ε_s are respectively the maximum ε and that at full turgor. Two sample comparisons were conducted to test for seasonal changes between measurement times.

3.2.5 Osmotic adjustment

Osmotic adjustment was calculated for both species as the difference between mean osmotic potential (π) in the R and I plots. Separate calculations were made at full and zero turgor for each measurement time. Decreases in π between the I and the R treatment represent osmotic adjustment while increases will be referred to as osmotic de-adjustment (Blake and Tschaplinski 1992).

3.2.6 Water potential isotherms and $d\psi/dR^*$

Water potential was plotted against relative water content, and for each tree the slope of this water release curve ($d\psi/dR^*$) was determined for the region of positive turgor by linear regression. Two sample comparisons (t-tests) were used to test for significant seasonal, water stress and species effects on $d\psi/dR^*$ in the region of positive turgor. This conservative approach was taken to avoid the problem of multiple points per observation (Snecedor and Cochran 1967, Draper and Smith 1981).

3.3 Results

3.3.1 Pre-dawn water potential and cumulative water stress integral

A stress cycle was defined as any period during which pre-dawn water potential (ψ_{max}) in the R treatment was significantly ($p<0.05$) lower than in the I treatment. Six such cycles occurred during the study (Table 3.1, Figure 3.1a). In the I treatment ψ_{max} remained higher than -0.5 MPa throughout (Figure 3.1a). From November 6, 1991, to April 30, 1993, ψ_{max} was measured on 37 occasions. On 23 of these ψ_{max} was significantly lower in the R than the I treatment. On April 30, 1993, at the completion of the experiment, the cumulative stress integral (S_ψ) for the R *E. globulus* and *E. nitens* was 229 and 225 MPa d respectively (Figure 3.1b).

Table 3.1. Minimum values of mean pre-dawn leaf water potential (ψ_{max} ,MPa) in the R treatment for each of 6 stress cycles.

Cycle, Date	*E. globulus*	*E. nitens*
1, December 10 1991	-0.59	-0.58
2, January 30 1992	-1.24	-2.01
3, July 1 1992	-0.57	-0.55
4, January 5 1993	-1.48	-1.31
5, February 19 1993	-0.88	-0.92
6, April 30 1993	-2.37	-2.34

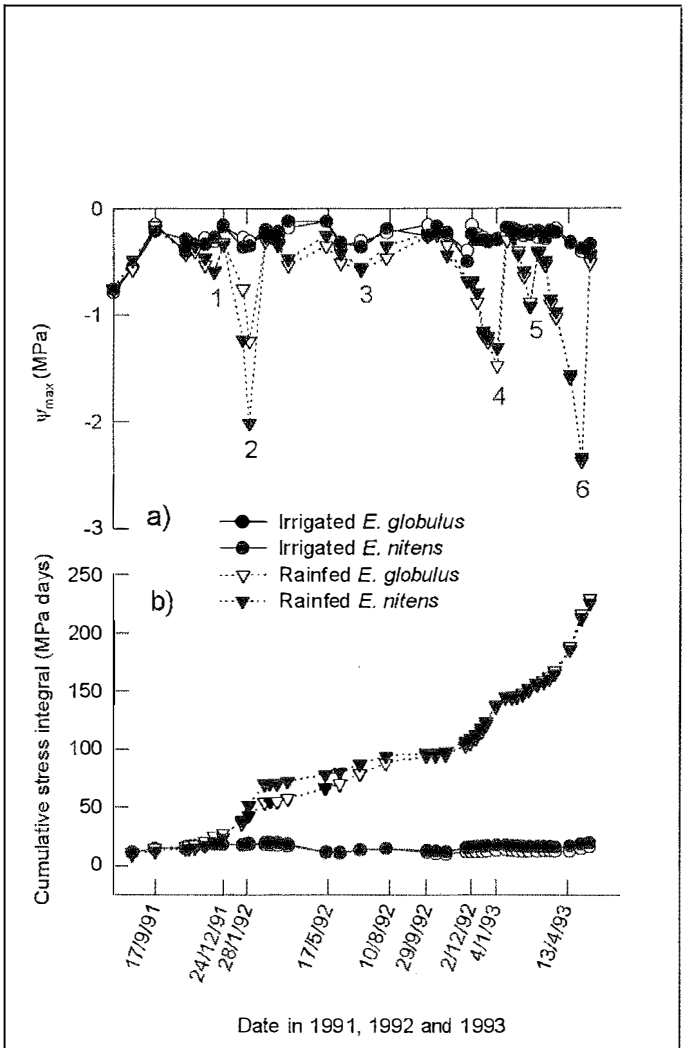

Figure 3.1. Indicators of water stress for the irrigated and rainfed treatments of *E. globulus* and *E. nitens* from July 22 1991 to April 30 1993. a) Pre-dawn water potential (stress cycles referred to in the text are numbered 1 to 6, see also Table 3.1) and b) Cumulative water stress integral

3.3.2 Seasonal variation (Irrigated treatment only)

In 1991/92 and 1992/93 osmotic potential (π) increased from a low value in early spring to a high value in December (Figure 3.2a and 3.2b). As each summer progressed, osmotic potential at full turgor (π_s) decreased slightly while osmotic potential at turgor loss point (π_p) tended to increase in *E. globulus* (Figures 3.2a and 3.2b). On September 17, 1991, and September 29, 1992, π_s and π_p of *E. nitens* were lower than at other times of the year. On September 29, 1992, π_s and π_p (-1.85 and -2.45 MPa respectively) were significantly lower in *E. nitens* than at any other time (Figures 3.2a and 3.2b). In *E. nitens* this spring reduction of osmotic potential was larger for π_p than π_s resulting in a small, non-significant, increase in the difference between π_s and π_p ($\Delta\pi$). At the same time π_s and π_p of *E. globulus* (-1.32 and -1.80 MPa respectively) were significantly higher ($p<0.05$) than in *E. nitens* (Figure 3.2a and 3.2b). On January 4, 1993, π_s in *E. globulus* was -1.29 MPa and increased to -1.11 MPa by April 13, 1993. During the same period π_s decreased from -1.24 to -1.50 MPa in *E. nitens*.

There was no consistent pattern for seasonal changes in bulk elastic modulus at full turgor (ε_s). The lower values of ε_s, 4 to 5 MPa, were similar for both species (Figure 3.2c). The higher values, however, were greater for *E. nitens*, about 10 MPa, than for *E. globulus,* about 8.5 MPa (Figure 3.2c). ε_s was significantly higher in *E. nitens* on September 29, 1992, December 24, 1992, and April 13, 1993, than at other times of the year. No significant seasonal changes in ε_S were evident for *E. globulus*. On September 29, 1992, and April 13, 1993, ε_s was significantly lower in *E. globulus* than *E. nitens* ($p<0.05$).

For much of the course of the experiment the slope of water release curves ($d\psi/dR^*$) in the region of positive turgor were between 10 and 12 MPa, and a tendency for *E. globulus* to have a higher water potential for a given relative water content than *E. nitens* was evident. This difference was rarely significant but was observed consistently throughout the experiment (Figure 3.3a-i). On September 17, 1991 (Figure 3.3a) and September 29, 1992 (Figure 3.3f) $d\psi/dR^*$ was significantly

higher for both treatments of both species than at other measurement times (Table 3.2).

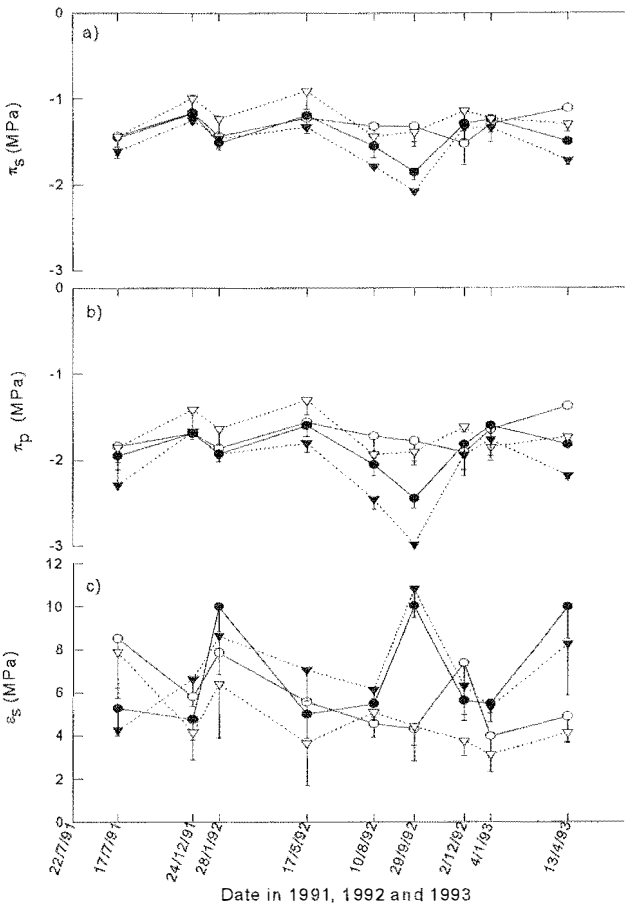

Figure 3.2. Tissue water relations variables for the irrigated and rainfed treatments of *E. globulus* and *E. nitens* from September 17, 1991, to April 13, 1993. a) $\pi_s \pm$ s.e. b) $\pi_p \pm$ s.e., and c) $\varepsilon_s \pm$ s.e.. Symbols as for figure 3.1.

3.3.3 Water stress

Osmotic potential was usually lower in the R trees than the I trees in *E. nitens* while the reverse was usually the case in *E. globulus* (Figure 3.2a and 3.2b). Maximum adjustment was observed on August 10, 1992, in *E. globulus* (-0.12 MPa) and on September 29, 1992, in *E. nitens* (-0.23 MPa).

At the end of January 1992 when ψ_{max} was -1.24 and -2.03 MPa in rainfed *E. globulus* and *E. nitens*, respectively (during stress cycle 2, Figure 3.1a), no significant effect of available water on tissue water relations variables was evident. On January 24 and April 13, 1993, at the end of stress cycles 4 and 6 respectively, $\Delta\pi$ was significantly higher in the R than in the I trees. Osmotic potential at full turgor (π_s) was significantly lower at the end of stress cycle 6 in the R than the I trees while the effect of water status on π_p was almost significant (Figures 3.2a and 3.2b). On December 24, 1991, and January 4, 1993, ε_s was higher in irrigated than rainfed *E. globulus*: the reverse was true for *E. nitens*. This contrast between the species resulted in a significant species by water status interaction for ε_s. In general, water stress reduced π_s and π_p in both species and increased ε_s in *E. nitens* while decreasing it in *E. globulus*.

At no stage did available water significantly influence the shape of the water release curve (Figure 3.3). Even on April 13, 1993, when rainfed trees were experiencing significant soil and tissue water deficits for the sixth time in the 18 months (Figure 3.1a), $d\psi/dR^*$ in the region of positive turgor was not significantly affected by water stress (Table 3.2, Figure 3.3i).

In general water stress tended to increase $\Delta\psi$. On December 9, 1991, at the bottom of stress cycle 1 mean $\Delta\psi$ was significantly higher for the R than the I treatment (Figure 3.4). On January 31, 1992, at the end of stress cycle 2 there was a significant species by water stress interaction on ψ_{min} (Figure 3.4). This occurred because ψ_{max} of the R *E. nitens* was below turgor loss point.

3.3.4 *E. globulus* v. *E. nitens*

Osmotic potential at full and zero turgor were consistently lower for *E. nitens* than *E. globulus* and for much of the experiment were lower in irrigated *E. nitens* than in rainfed *E. globulus* (Figures 3.2a and 3.2b). π_s and π_p were significantly lower in *E. nitens* than *E. globulus* in April 1993. Trends in ε_s were less consistent than trends in osmotic potential. During stress cycles in January 1992 and April 1993 ε_s was

much higher for *E. nitens* (9.5 and 9.5 MPa) than *E. globulus* (6.5 and 4.2 MPa). In general, rainfed *E. globulus* had the lowest ε_s throughout the course of the experiment.

On September 29, 1992, mean $d\psi/dR^*$ was significantly ($p<0.05$) higher for *E. nitens* (18.1 MPa) than for *E. globulus* (14.7 MPa). On April 13, 1993, significant differences between the species were also apparent and were now highly significant ($p<0.001$). The mean value for *E. nitens* was 14.6 MPa compared with 9.2 MPa for *E. globulus* (Table 3.2). At the same time, $d\psi/dR^*$ beyond the turgor loss point was almost identical for the two species, although in this region ψ ($\psi=\pi$) was significantly higher for *E. globulus* than for *E. nitens* for any given R*.

Table 3.2. Mean $d\psi/dR^*$ (MPa) in the region of positive turgor by species and water status in September 1991, December 1991, September 1992 and April 1993.

Treatment	Irrigated *E. globulus*	Irrigated *E. nitens*	Rainfed *E. globulus*	Rainfed *E. nitens*
Sep 1991	15.14	12.18	13.52	15.15
Dec 1991	10.65	10.36	10.11	11.88
Sep 1992	14.69	18.45	14.67	17.93
Apr 1993	9.72	14.10	8.71	15.09

In general, positive turgor was maintained over a greater range of relative water content by *E. globulus* than by *E. nitens* and this difference was most apparent on April 13, 1993, when turgor loss occurred at an average R^*_p of 0.87 for *E. nitens* and 0.79 for *E. globulus* (Figure 3.5a). At the same time a reduction in dP/dR^* above $R^*=0.95$ for *E. globulus* occurred. As R* fell from 1.0 to 0.95 turgor pressure was almost unaffected by water content in *E. globulus* but was reduced from 1.6 MPa to 1.2 MPa in *E. nitens* (Figure 3.5a). Plotting ε against P for April 13, 1993 showed a decline in ε above a turgor pressure (P) of 0.6 and 0.75 MPa in the I and R *E. globulus* respectively (Figure 3.5b). ε_s was higher for *E. nitens* than *E. globulus* and within species, was higher in the rainfed treatment of the former and the irrigated treatment of the latter.

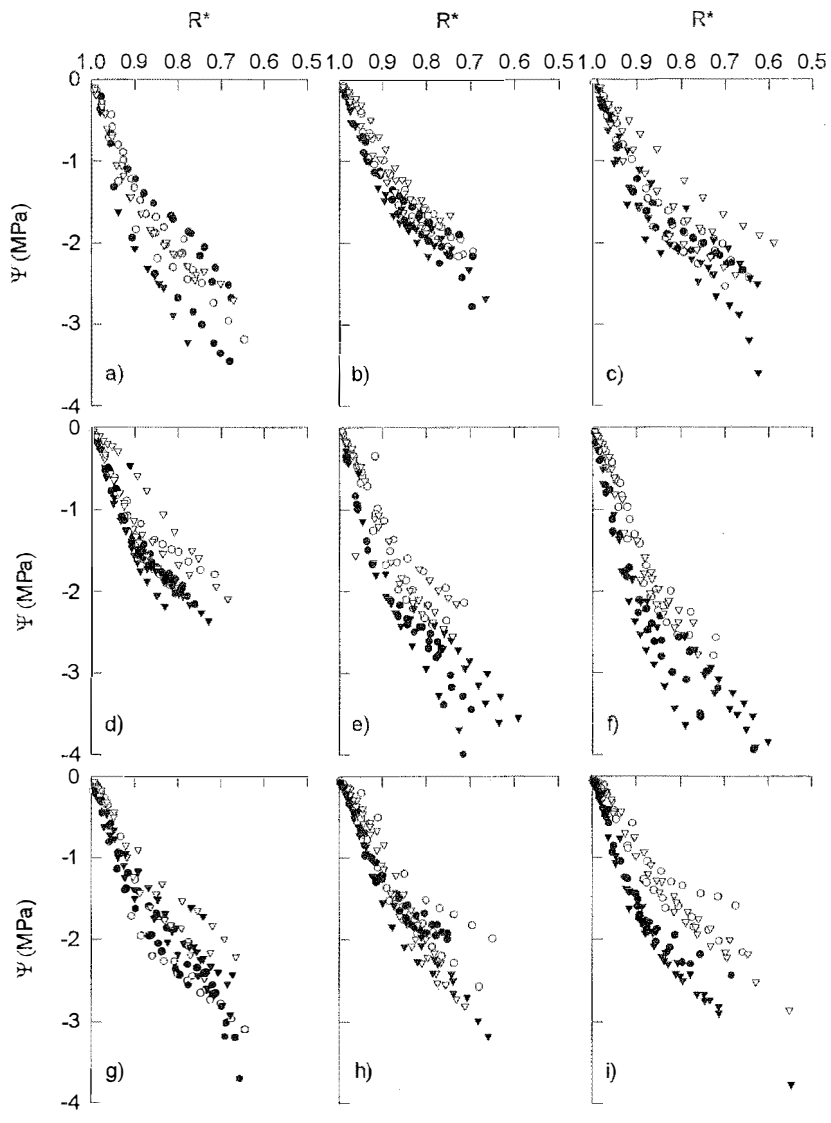

Figure 3.3. Water potential (ψ) versus relative water content (R*) for the irrigated and rainfed treatments of *E. globulus* and *E. nitens* in a) September 1991, b) December 1991, c) January 1992, d) May 1992, e) August 1992, f) September 1992, g) December 1992, h) January 1993 and i) April 1992. Symbols as for Figure 3.1.

Throughout the period for which it was measured, $\Delta\psi$ was significantly greater for *E. nitens* than for *E. globulus* (Figure 3.4)

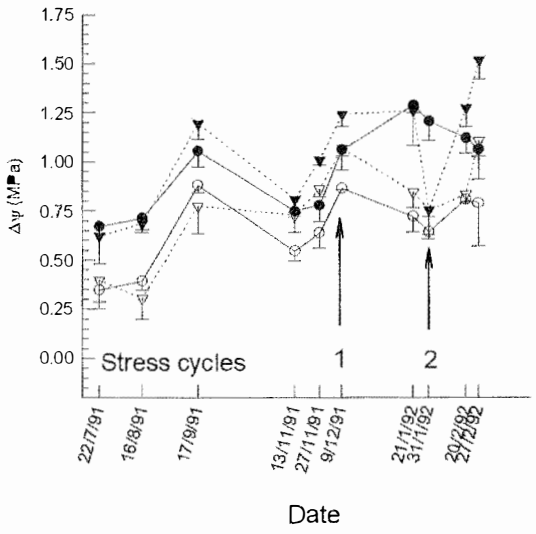

Figure 3.4. The mean (n=3) difference between pre-dawn and midday leaf water potential ($\Delta\psi \pm$ s.e.) for I and R *E. globulus* and *E. nitens* on 10 days between July 22, 1991, and February 27, 1992. Symbols as for Figure 3.1.

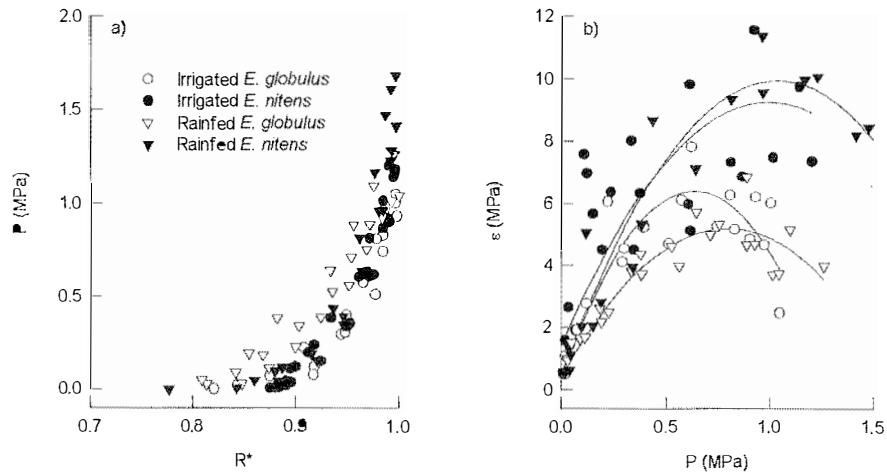

Figure 3.5. a) Turgor pressure (P) versus relative water content (R*) and b) Bulk elastic modulus (ε) versus turgor pressure (P) for the irrigated and rainfed treatments of *E. globulus* and *E. nitens* in April 1993. Lines on Fig 3b are second order polynomials fitted separately for both treatments of both species.

3.4 Discussion

Species was a more important determinant of drought response than the cumulative water stress imposed over the course of the experiment. It was initially hypothesised that *E. nitens* would be more drought tolerant than *E. globulus*. The results were to the contrary and suggest that *E. nitens* is more sensitive to drought than *E. globulus*. Moreover, traits which confer cold tolerance on *E. nitens* facilitate desiccation avoidance rather than drought tolerance. These principal results are discussed against the background of underlying seasonal variation.

3.4.1 Underlying seasonal variation (Irrigated treatment)

No significant seasonal variation in π_s or π_p was observed for *E. globulus*. In contrast, on September 17, 1991 and September 29, 1992, early spring in Tasmania, π_s and/or π_p were lower (significantly in 1992) for *E. nitens* than at other times of the year. This seasonal osmotic adjustment in *E. nitens* was accompanied by significant increases ($p<0.05$) in ε_s, $d\psi/dR^*$ and $\Delta\pi$, all of which are consistent with winter hardening. The natural distributions of *E. nitens* on high altitude sites subject to winter snow falls (Pederick 1979) and *E. globulus* below 300 m a.s.l. (Kirkpatrick 1974) support this interpretation. In a study of six *Eucalyptus* species, including *E. globulus* and *E. nitens*, there was little difference between species in frost hardiness at the end of May, late autumn, but by August, the end of winter, *E. nitens* had hardened to a greater extent than *E. globulus*. The degree of hardening between May and August was correlated with the minimum temperature experienced at each of the sites studied (Hallam et al. 1989). Frost is rare at the experimental site used here but eucalypts harden at temperatures below 4°C (Harwood 1980) and such temperatures were experienced during the study period. In several coniferous species, π was lowest at the end of winter or early spring and increased during the spring growth flush before declining again during the summer (Ritchie and Shula 1984, Teskey et al. 1984, Kubiske and Abrams 1991a, b, Colombo and Teng 1992). Ritchie and Shula (1984) attributed winter reduction in π_s and π_p of *Pseudotsuga menzeisii* (Mirb.) Franco needles (-2.3 and -3.8 MPa respectively) to accumulation of sugars and summer minima (-2.5 and -3.5

MPa respectively) to reduced symplasm volume. In *Picea abies* (L.) Karst there was no accumulation of osmotically active substances during winter and the observed reductions in π_s and π_p were attributed to a change in volume of the symplasm rather than to any change in solute content (Gross and Koch 1991). The absolute value of π at any given R* is directly proportional to solute content and inversely proportional to symplasmic volume (Tyree and Hammel 1972, Cheung et al. 1975). The significant decrease in π_S observed in *E. nitens* points to a higher concentration of solutes in the symplasm (Cheung et al. 1975). Increased W_d/W_t (results not shown) implies that part of the change in π_s is due to reduced symplasmic volume whereas the accompanying increase in $\Delta\pi$ may either be due to an increase in ε or to an absolute increase in solute content.

3.4.2 Water stress

Towards the end of the experiment, and after several cycles of drought, $\Delta\pi$ was significantly larger in R than in I treatments, though neither π_s nor π_p were significantly influenced by water stress at any stage. There were small non-significant reductions in π_s and π_p in the R treatment of *E. nitens*, but no consistent pattern for *E. globulus*, relative to the I treatment. Water stress cycles tended to increase ε_s in *E. nitens* but decrease it in *E. globulus*. There was thus no evidence of significant osmotic adjustment or de-adjustment in either species when simultaneous p-v curves for I and R treatments were compared.

Many previous studies with seedlings have reported significant reductions in osmotic potential due to water stress (eg. Parker and Pallardy 1988) but an absence of suitable controls in many field studies (eg. Sinclair 1980, Parker et al. 1982, Attiwill and Clayton-Greene 1984) has made it difficult to distinguish osmotic adjustment due to drought from underlying seasonal trends. In the current study, if osmotic potential of the R treatment of *E. nitens* in April 1993 had been compared to same the treatment in January 1993, rather than to the I treatment in April 1993, then a significant osmotic adjustment due to water stress would have been erroneously concluded. Much of the change in osmotic potential occurred in the I as well as the R treatment.

The absence of a pattern in osmotic or elastic adjustments in either *E. globulus* or *E. nitens* is consistent with statements made in recent reviews (Munns 1988, Blake and Tschaplinski 1992) in which the adaptive significance of such adjustments is questioned, particularly in plants such as trees which store little water and where water uptake is driven almost exclusively by atmospheric evaporative demand (Schulte 1992). Maintenance of gas exchange and expansive growth may not be well correlated with turgor maintenance. For example, stomatal closure in wheat in response to drying soil was independent of turgor pressure in the leaf (Gollan et al. 1986) and Feng et al. (1994), in a consideration of osmotic and elastic adjustments in the context of Lockhart's equation (Lockhart 1965), stressed that leaf expansion was often poorly correlated with turgor pressure because cell wall properties were also altered in response to water stress. In the current study, the tissue water relations of neither species acclimated to water stress.

3.4.3 Differences between the species

Throughout the experiment *E. globulus* tended to have lower ε_s, R^*_p and $d\psi/dR^*$ and higher π_s and π_p than *E. nitens*. On January 28, 1992, and April 13, 1993, the effect of species on $d\psi/dR^*$, R^*_p and π_s was significant ($p<0.05$). Values of π_s varied between -1.1 and -1.4 MPa in *E. globulus* and -1.1 and -2.1 MPa in *E. nitens*. The lowest value of π_s, when adjustments due to frost hardening were ignored, was -1.72 MPa. Values of π_s for the less mesic eucalypts *E. melliodora* A. Cunn. ex Schau. (-2.18 MPa) and *E. microcarpa* Maiden (-2.6 MPa) and *E. behriana* F. Muell., *E. microcarpa* and *E. polyanthemos* Schau. under well-watered (-1.74, -1.65 and 1.62 MPa respectively) and water-stressed (-1.93, -1.98 and -2.14 MPa respectively) conditions (Clayton-Greene 1983, Myers and Neales 1986) were more negative than those found here which were comparable with those found for *E. globulus* seedlings in Portugal (Correia et al. 1989). Ladiges (1975) reported a range of values for mature *E. viminalis* Labill., a mesic species, similar to those observed in *E. nitens* in the current study.

Differences between *E. globulus* and *E. nitens* were most pronounced near the end of the experiment on April 13, 1993, when $d\psi/dR^*$ in the region of positive turgor

was significantly greater for *E. nitens* than *E. globulus* (Figure 3.3i). Thus for any given ψ, R* was significantly higher for *E. nitens* than *E. globulus*. At the same time ε_s was greater for *E. nitens* and a reduction in R* from 1 to 0.9 resulted in a corresponding reduction in turgor pressure of approximately 0.3 MPa in *E. globulus* and 1.8 MPa in *E. nitens* (Figure 3.5a). Stomatal conductance and growth were found to be more sensitive to water stress in *E. nitens* than *E. globulus* (White et al. 1994a, b). Maintenance of high R* at low ψ in *E. nitens* therefore seems to be a means of avoiding desiccation whereas in *E. globulus*, lower ε facilitates maintenance of turgor over a wider range of R* and allows *E. globulus* to tolerate moderate water stress. The association of lower π in *E. nitens*, than in *E. globulus*, with gas exchange and growth processes which are more sensitive to water stress highlights the need to consider both osmotic and elastic properties in studies of tissue water relations. Feng et al. (1994) suggested that cell wall extensibility rather than osmotic properties might be adjusted in response to water stress in spring wheat. Their assertion was based on the observation that lower osmotic potentials in sudangrass, compared to spring wheat, were associated with a greater sensitivity of leaf expansion to water stress. Robichaux et al. (1983) reported similar differences in the elastic properties of *Dubautia scabra* and *D. ciliolata* to those found for the eucalypts here. *D. ciliolata* had a lower ε allowing it to maintain positive turgor at lower values of R* than *D. scabra*.

In a study of variation among populations of *E. viminalis*, seedlings from a low rainfall granite site had lower π and higher $d\psi/dR^*$ than either of two populations from more mesic environments (Ladiges 1975). In contrast to the current study, lower π and higher $d\psi/dR^*$ for the low rainfall populations of *E. viminalis* were accompanied by a capacity to maintain transpiration at lower soil water contents than in the more mesic populations (Ladiges 1974). Clayton-Greene (1983) reported much higher values of $d\psi/dR^*$ in the region of positive turgor for *E. microcarpa* (21.4 MPa) and *E. melliodora* (22.3 MPa) than for *Callitris columellaris* F. Muell. (13.0 MPa). Below R^*_p, $d\psi/dR^*$ increased dramatically to be much greater in *C. columellaris* than in the eucalypts. This increase was interpreted as development of a high desiccation resistance in *C. columellaris*.

Interestingly, in *E. microcarpa* and *E. melliodora* the quite high values of $d\psi/dR^*$ in the region of positive turgor were associated with the maintenance of gas exchange at leaf water potentials as low as -5.5 MPa, whereas in the current study the same trait was associated with drought avoidance and low stomatal conductance in *E. nitens* (see chapter 6). On April 13, 1993 there was no significant difference between *E. globulus* and *E. nitens* in the value of $d\psi/dR^*$ below the turgor loss point, although by virtue of a higher slope above the turgor loss point, the absolute value of water potential for any given R* was significantly lower for *E. nitens* than for *E. globulus* (Figure 3.3i). This difference may result in greater resistance to desiccation in *E. nitens* than *E. globulus* when exposed to more extreme water stress than in the current study but this was not tested. The association of buffering by bound water with drought resistance (Gaff and Carr 1961, Pook et al. 1966) seems less significant for *E. nitens* than resistance to desiccation resulting from the elevated solute contents associated with cold tolerance.

Maintenance of positive turgor over a wider range of R* by *E. globulus* than by *E. nitens* might be anticipated to result in higher growth rates under conditions of water stress. Expansive growth is very sensitive changes in turgor pressure (Acevedo et al. 1971, Hsiao et al. 1976, Bradford and Hsiao 1982) and a greater reduction in relative diameter growth due to water stress was observed in *E. nitens* than *E. globulus* (White et al. 1994a). This lower growth rate in *E. nitens* was probably mediated by a combination of lower stomatal conductance and the effects of turgor pressure and cell wall elasticity on growth.

The interspecific differences observed in the leaf water relations of *E. globulus* and *E. nitens* were manifested as a significantly higher midday water potential in the former species. It is likely that the consistently lower daytime leaf water potential and a greater gradient of water potential from root to leaf will ultimately reduce the hydraulic conductivity of *E. nitens* in comparison to *E. globulus* (Whitehead et al. 1984). This may have some impact on relative capacities of the two species to recover after alleviation of water stress, a hypothesis which will be explored further in subsequent chapters.

Chapter 4. Development of leaf area index and relationships between leaf area and conducting sapwood area

4.1 Introduction

Estimates of leaf area and its distribution within the canopy are important from several perspectives. Firstly, they are necessary for calculation of canopy conductance and transpiration from either stomatal conductance or sapflux of individual trees (Jarvis et al. 1981). Secondly, water stress will affect yield by reducing leaf initiation and expansion (Metcalfe et al. 1989). Thirdly, canopy structure regulates the light, wind and moisture environments of the subcanopy and forest floor.

Approaches for estimating leaf area and leaf area index are either direct or indirect. Indirect measurements relate the radiation environment below the canopy to leaf area assuming a particular distribution of foliage (Norman and Campbell 1989). Direct methods rely on leaf sampling and/or litter collection. Where indirect and direct measurements of leaf area have been compared for forest canopies, the indirect approach has seriously underestimated leaf area (Chason et al. 1991, Smith et al. 1993). A major limitation is adequate characterisation of the distribution of foliage (Smith et al. 1993). While direct determination of leaf area is time consuming and necessitates interpolation between sampling times, it remains the most reliable means of determining leaf area. The most common approach has been to adopt the pipe model interpretation of plant form (Shinozaki et al. 1964a) and develop allometric relationships between leaf mass or leaf area (A_l) and sapwood area (A_s) (eg. Grier and Waring 1974, Whitehead and Jarvis 1981).

The pipe model interpretation of plant form implies a causal relationship between A_l and A_s. While the direction of causation remains unclear, most studies have found a

strong positive correlation between A_l and A_s measured at breast height. The resultant, usually linear, relationships between A_l and A_s have served as useful predictors of A_l in conifers (Whitehead and Jarvis 1981, Waring et al. 1982), deciduous hardwoods (Rogers and Hinckley 1979, Burton et al. 1991) and eucalypts (Beadle and Mummery 1989). The slope parameter (A_l:A_s) has provided a physiological measure for interpreting changes in leaf area with conducting area. It has been observed to vary with species (Grier and Waring 1974, Kaufmann and Troendle 1981), site quality (Whitehead 1978, Brix and Mitchell 1983), stand vigour (Espinosa Bancalari et al. 1987) and density (Keane and Weetman 1987), water availability (Grier and Running 1977) and average vapour pressure deficit (Mencuccini and Grace 1995). At first the task of resolving the effects of this suite of driving variables on A_l:A_s appears rather intractable. However, the notion of equating transpiration, as predicted by a form of the Penman-Monteith equation, with volumetric flow rate predicted by Darcy's law (Whitehead et al. 1984) gives the relationship:

$$\frac{A_l}{A_s} = \frac{k_h(\Delta\Psi/l)c}{Dg_s} \qquad (4.1)^1$$

This has provided a framework for interpreting variation in A_l/A_s of a stem of length (l) in terms of the water potential gradient over that length ($\Delta\psi$), hydraulic conductivity (k_h) and time averaged vapour pressure deficit (D) and stomatal conductance (g_s). Within this framework, physiological differences between *E. globulus* and *E. nitens* grown under irrigated and water limited conditions have the potential to affect the relationships amongst A_l/A_s, $\Delta\psi$ and k_h. Quantifying these effects is a critical first step in describing the instantaneous and cumulative effect of water stress on leaf area development in *E. globulus* and *E. nitens*.

To date, consideration of the effect of water stress on leaf area development in *Eucalyptus* spp. has been restricted to seedlings (eg. Metcalfe et al. 1989) while

[1] The coefficient $c = \lambda\gamma\rho_w/(\eta c_p\rho_a)$, where λ is the latent heat of vaporisation of water, γ is the psychrometric constant, ρ_w and ρ_a are the density of water and air respectively, η is the viscosity of water and c_p is the specific heat of air.

allometric relationships between leaf area and sapwood area have been derived for developing *E. nitens* canopies (Beadle and Mummery 1989). In the present chapter the influence of species and water stress on the parameters of these relationships in a plantation of *E. globulus* and *E. nitens* at age two and three years is considered. The relationships are applied to sapwood area data to plot the course of leaf area index from age one to three years for these species when managed under irrigated and water-limited conditions.

4.2 Materials and Methods

4.2.1 Leaf area

In May 1992 trees in the growth plots of the I and R treatments of each species were allocated to one of six size classes on the basis of diameter (d_t) and height (h_t), using the formula $d_t^2 h_t$. Twenty four trees were selected for leaf area determination, six from the I and R treatment of each species. Two trees were selected from the buffer zone of each block so that all six size classes were represented in each species by treatment combination. The size classes taken from each block were assigned at random. Diameter over bark at 0.15 m and 1.3 m and height were measured for each tree. Each tree was divided into six canopy zones, three layers (the upper, middle and lower third by depth)[2] by two aspects (east and west). The foliage was removed and specific leaf area (SLA) calculated for a sub-sample of leaves from each zone on the basis of oven-dry weight at 80°C. SLA was calculated on a single sided or projected leaf area basis[3]. The remaining leaves were similarly dried. The leaf area of each zone of each tree was calculated as the product of total leaf dry weight and SLA. Sapwood area was calculated as the basal area at 0.15 or 1.3 m. No heartwood was present.

This process was repeated in July 1993. The method of tree selection was the same as in 1992 but a few changes were made to the procedure for leaf area

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[2] The canopy was divided up in this way so that canopy conductance and transpiration could be calculated using a multiple layer formulation of the Penman-Monteith equation (Monteith 1965). The relative merits of multiple versus single layer models are considered further in Chapters 5 and 7.

[3] Unless otherwise stated leaf area indices reported or discussed are projected or single sided.

determination. After a subsample was removed for determination of SLA, the remaining leaves were dried to constant weight at 40°C. A subsample of this bulk leaf mass was weighed separately (W_{40}) and then dried at 80°C before reweighing (W_{80}). The bulk leaf weight was multiplied by the ratio W_{80}/W_{40} to give an oven-dry equivalent. In 1993 diameter was only measured at 1.3 m. Again sapwood area was calculated as the basal area at 1.3 m since no heartwood was present.

Noticeable leaf fall occurred between April 1993 and July 1993, particularly in the irrigated *E. nitens*. When the trees were harvested leaf litter was collected from a 7 m^2 area (3.5 x 2 m) centered on each sampled tree. The total area of the leaves in the litter was calculated and allocated to each size class as a constant proportion of the total green leaf area remaining in the stand.

4.2.2 Analysis and calculation of leaf area index (L*)

A t-test for unpaired data was used to investigate the effect of treatment (I vs R) and species on SLA. Correlation and regression analyses were used to examine the distribution of leaf area within the canopy by layer and aspect. Linear regression was used to develop relationships between leaf area in 1992 and sapwood area at 0.15 m and 1.3 m and between leaf area in 1993 and sapwood area at 1.3 m.

The relationships developed between leaf area and sapwood area were used to calculate the leaf area of all growth plot trees. Individual tree leaf areas were summed over the entire growth plot and the resultant total area projected on the plot area (210m^2) to give an estimate of leaf area index (L*) for each growth plot. This process was repeated for growth measurements collected with varying regularity between June 1991 and June 1993 to plot the course of L* throughout development of the plantation. These growth data are reported and discussed in Honeysett et al. (1996). Analysis of variance was used to test for significant effects of treatment (I vs R) and species on L* assuming a randomised block design with two strata. The treatment term was included in the upper (block) stratum and tested against a residual with four degrees of freedom. The species and interaction terms

were included in the lower stratum and tested against a different residual, also with four degrees of freedom.

4.3 Results

4.3.1 Specific leaf area

Specific leaf area (SLA) was significantly higher in 1992 than in 1993 for all canopy layers. Mean SLA across all species, treatments and layers was 8.2 and 6.3 m^2 kg^{-1} in 1992 and 1993 respectively. In both years SLA increased with canopy depth (Table 4.1). There was no effect of aspect on SLA in either year.

In 1992 SLA was significantly higher ($p<0.05$) in the I than the R treatment in the upper (8.4 and 7.5 m^2 kg^{-1}) , middle (8.5 and 7.3 m^2 kg^{-1}) and almost significantly higher ($p=0.055$) in the lower third (9.4 and 8.3 m^2 kg^{-1}) of the canopy. SLA was higher in *E. globulus* than *E. nitens* in all canopy layers (Table 4.1) although this difference was only significant ($p<0.05$) in the bottom third. In 1993 SLA remained higher in the I than the R treatments for all canopy layers although this difference was no longer significant. SLA was significantly higher in *E. nitens* than *E. globulus* for all but the bottom layer of the canopy (Table 4.1).

Table 4.1. Mean specific leaf area (m^2 kg^{-1}) across all size classes for the I and R treatments of *E. globulus* and *E. nitens* in 1992 and 1993, summarised by canopy layer.

	Upper canopy		Mid Canopy		Lower Canopy	
	1992	1993	1992	1993	1992	1993
I *E. globulus*	8.5	4.9	8.7	6.0	10.5	8.2
I *E. nitens*	8.4	5.4	8.4	6.6	8.5	8.4
R *E. globulus*	7.6	4.4	7.3	5.3	8.9	7.3
R *E. nitens*	7.4	5.1	7.2	6.3	7.7	7.5

4.3.2 Distribution of leaf area

Aspect. No consistent pattern in the distribution of leaf area between the eastern and western halves of the canopy was observed. Data for the two aspects were pooled for consideration of the vertical distribution of leaf area.

Layer. Correlations between leaf area in the upper, middle and lower third of the canopy and sapwood area at 1.3 m were variable and often low, ranging from 0.06 to 0.97 in 1992 and 0.10 to 0.93 in 1993. Consequently the proportion of total leaf area in the upper, middle and lower canopy layers (l_u, l_m and l_l) was calculated and regressed on sapwood area at 1.3 m. In 1992 the slopes of the resultant relationships between l_u, l_m, l_l and A_s were significantly different from zero in the R treatment but not in the I treatment. In 1993 the slopes of these relationships were not significantly different from zero in either treatment of either species. In both years the y-intercept was a much more important determinant of l_u, l_m and l_l than sapwood area resulting in relatively constant values across a range of sapwood areas[4]. Mean l_u, l_m and l_l across treatments and species were 0.13, 0.41 and 0.46 in 1992 and 0.11, 0.36 and 0.53 in 1993 (Table 4.2).

Table 4.2. Proportion of leaf area in the upper, middle and lower third of the canopy by species and treatment in 1992 and 1993.

	Upper		Middle		Lower	
	1992	1993	1992	1993	1992	1993
I *E. globulus*	0.09	0.13	0.37	0.40	0.54	0.47
I *E. nitens*	0.16	0.08	0.42	0.32	0.42	0.60
R *E. globulus*	0.13	0.12	0.36	0.35	0.51	0.54
R *E. nitens*	0.13	0.11	0.47	0.35	0.40	0.54

Litter. The mean area of leaf litter collected was significantly greater for *E. nitens* than *E. globulus* and was significantly greater for I than R trees. Mean area of leaf

[4]In order to estimate stomatal conductance or transpiration at the canopy scale it is desirable to divide the canopy into layers but impractical to measure sapwood area at more than one level. In this context the observation that l_u, l_m and l_l were relatively stable across the range of sapwood areas measured is very useful. In chapter 5 and 6 total canopy L* will be apportioned to each of three canopy layers of equal depth using the values for l_u, l_m and l_l in Table 4.4 in order to calculate canopy stomatal conductance and transpiration. L* is not presented layer by layer in this chapter.

litter per tree in the I and R treatments was, respectively, 5.0 and 3.0 m^2 in *E. globulus* and 16.6 and 7.1 m^2 in *E. nitens*.

4.3.3 Leaf area v. sapwood area

July 1992. In 1992 leaf area was strongly correlated with sapwood area at 0.15 m and coefficients of determination (r^2) ranged from 0.90 to 0.97 (Table 4.3). Species rather than treatment determined the slope and y-intercept of the relationships. The effect of species on the slope of the relationships was almost significant ($p=0.062$). Irrigation increased the slope but only from 0.71 to 0.79 in *E. globulus* and 0.53 to 0.55 in *E. nitens* (Table 4.3). Values of r^2 were also high for relationships between leaf area and sapwood area at 1.3 m except for the irrigated *E. nitens* (0.72). Differences between species and treatments were the same as for relationships at 0.15 m.

As neither y-intercept nor slope was significantly influenced by irrigation the data for the I and R treatments was pooled and separate relationships developed for each species (Figures 4.1 a and b).

Table 4.3. Slopes, intercepts and coefficients of determination (r^2) for relationships between leaf area (A_l, m^2) and sapwood (A_s, cm^2) area 0.15 and 1.3 m above ground in July 1992, by species and treatment and by species only.

Height of A_s	Treatment and species	Intercept	Slope	r^2
0.15 m	Irrigated *E.globulus*	-5.39	0.79	0.90
	Irrigated *E.nitens*	-2.02	0.55	0.97
	Rainfed *E.globulus*	-3.67	0.71	0.94
	Rainfed *E.nitens*	-1.59	0.53	0.94
	E.globulus (I & R)	-4.63	0.76	0.93
	E.nitens (I & R)	-1.87	0.54	0.96
1.3 m	Irrigated *E.globulus*	1.92	1.17	0.94
	Irrigated *E.nitens*	3.72	0.81	0.72
	Rainfed *E.globulus*	5.67	0.96	0.96
	Rainfed *E.nitens*	3.48	1.29	0.91
	E.globulus (I & R)	3.99	1.06	0.95
	E.nitens (I & R)	4.71	0.85	0.72

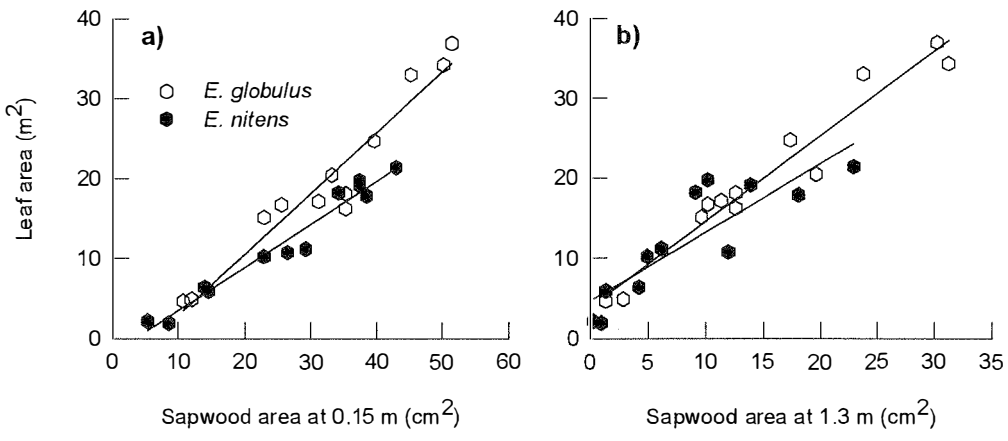

Figure 4.1. Leaf area versus sapwood area a) 0.15 m and b) 1.3 m above ground, in July 1992. Lines fitted are linear regressions of leaf area (m^2) on sapwood area (cm^2) for *E. globulus* and *E. nitens*. The I and R data within species were pooled.

July 1993. The mean slope (across species and treatments) of relationships between leaf area and sapwood area at 1.3 m above ground was significantly lower in July 1993 (0.57) than July 1992 (1.06).

Leaf area including litter was still strongly correlated with sapwood area at 1.3 m although values of r^2 were lower (between 0.53 and 0.81) than in 1992 (Table 4.3). In contrast to 1992, slope was decreased appreciably by irrigation (p=0.12) from 0.70 to 0.48 in *E. globulus* and 0.61 to 0.47 in *E. nitens*. The effect of species on slope had become less important than in 1992 (p=0.45). The results were similar when litter was excluded.

The data for the species were pooled and separate relationships fitted for the I and R treatments (Figure 4.2). Relationships were developed including and excluding the contribution of litter collected in July 1993. Exclusion of litter increased the intercept and the slope (Table 4.4, Figure 4.2).

Table 4.4. Slopes, intercepts and coefficients of determination (r^2 values) for relationships between leaf area (m^2) and sapwood area 1.3 m above ground (cm^2) in July 1993, by species and treatment including litter (unshaded), and by treatment only (data for both species within treatment pooled, shaded) including and excluding litter.

Dataset	Intercept	Slope	r^2
Irrigated *E.globulus*	11.3	0.48	0.53
Irrigated *E.nitens*	15.7	0.47	0.68
Rainfed *E.globulus*	7.6	0.7	0.76
Rainfed *E.nitens*	10.76	0.61	0.81
Irrigated - litter	14.56	0.46	0.63
Irrigated + litter	8.57	0.39	0.44
Rainfed - litter	10.03	0.64	0.82
Rainfed + litter	6.23	0.60	0.85

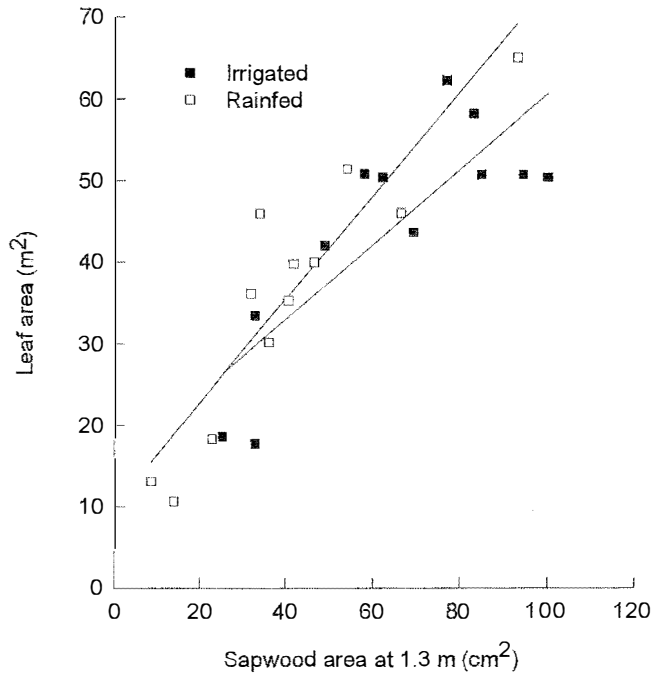

Figure 4.2. Leaf area versus sapwood area at 1.3 m in July 1993. Lines fitted are linear regressions of leaf area (m^2) on sapwood area (cm^2) for the I (closed squares) and R (open squares) treatment. *E. globulus* and *E. nitens* data within treatment were pooled.

4.3.4 Leaf area development

*4.3.4a Calculation of L**

The relationships presented in section 4.3.3 were used to calculate L* for the I and R treatment of both species. The different sets of relationships for 1992 and 1993 were applied as follows.

1. Prior to September 1992 leaf area (A_l) was calculated separately for the two species using sapwood area at 0.15 m (Table 4.2, Figure 4.1).

2. From September 1992 to June 1993 A_l was calculated from sapwood area at 1.3 m (breast height). Leaf area was calculated a) by species using the relationships developed in 1992 (Table 4.2, $A_{l,92}$) and b) by treatment from relationships developed in 1993 including litter (Table 4.3, $A_{l,93}$). Actual leaf area was then calculated for the I and R treatment of *E. globulus* and *E. nitens* as a weighted

average of $A_{1,92}$ and $A_{1,93}$. Weighting was done using days since July 1 1992 (d) as follows.

$$A_1 = A_{1,92}\left(1-\frac{d}{365}\right)+A_{1,93}\left(\frac{d}{365}\right) \quad (4.2)$$

3. In all cases L* was calculated as described in the methods section of this chapter

4.3.4b Seasonal trends.

In the I plots maximum leaf area development occurred between late September and late March in 1991/92 and 1992/93. By April 1993 L* was 8.3 and 6.9 in the I treatments of *E. nitens* and *E. globulus* respectively (Figure 4.3, Table 4.5). These figures coincide with canopy closure and probably represent the maximum values of L* observed in the plantation. At this point litter fall increased dramatically, particularly in the I *E. nitens* making later estimates of L* difficult to interpret.

Table 4.5. Mean leaf area index (L*) ± se. for I and R *E. globulus* and *E. nitens* at Age 2 and 3 years.

	Irrigated *E. globulus*	Irrigated *E. nitens*	Rainfed *E. globulus*	Rainfed *E. nitens*
June 1992 (Age 2)	3.2 ± 0.5	2.1 ± 0.2	2.7 ± 0.1	1.6 ± 0.3
April 1993 (Age 3)	8.3 ± 0.1	6.9 ± 0.6	6.1 ± 0.3	4.3 ± 0.4

4.3.4c Species.

From November 1991 to June 1993 L* was significantly lower for *E. nitens* than *E. globulus* (Figure 4.3). Until February 1993 L* was greater for R *E. globulus* than for I *E. nitens*. In autumn and early winter of 1993 leaf fall was greater in the I *E. nitens* than in the other treatments.

4.3.4d Water stress.

After November 1992 L* was significantly lower in the R than the I treatment (Figure 4.3). Prior to this, the effect of treatment on L* was evident but non-significant. From July 1992 to June 1993 the relative effect of water stress on leaf

area index was slightly greater for *E. nitens* than *E. globulus*. Over this 12 month period the ratio of L* in the R to L* in the I treatment decreased from 0.80 to 0.62 in *E. nitens* and 0.84 to 0.74 in *E. globulus*. The greater relative and absolute effect of water stress on L* in *E. nitens* compared to *E. globulus* did not result in a significant treatment by species interaction with respect to L*.

The pattern of reduction in L* due to water stress differed markedly between the species. In *E. nitens* reduction in L* of the R relative to the I blocks was steady and cumulative while in *E. globulus* the pattern was stepped. After rainfall in early January 1993 L* increased rapidly in the R *E. globulus* before decreasing sharply after a further month without significant rainfall or supplementary irrigation. The same 40 mm rainfall event had less impact on leaf area development of the R *E. nitens* (Figure 4.3).

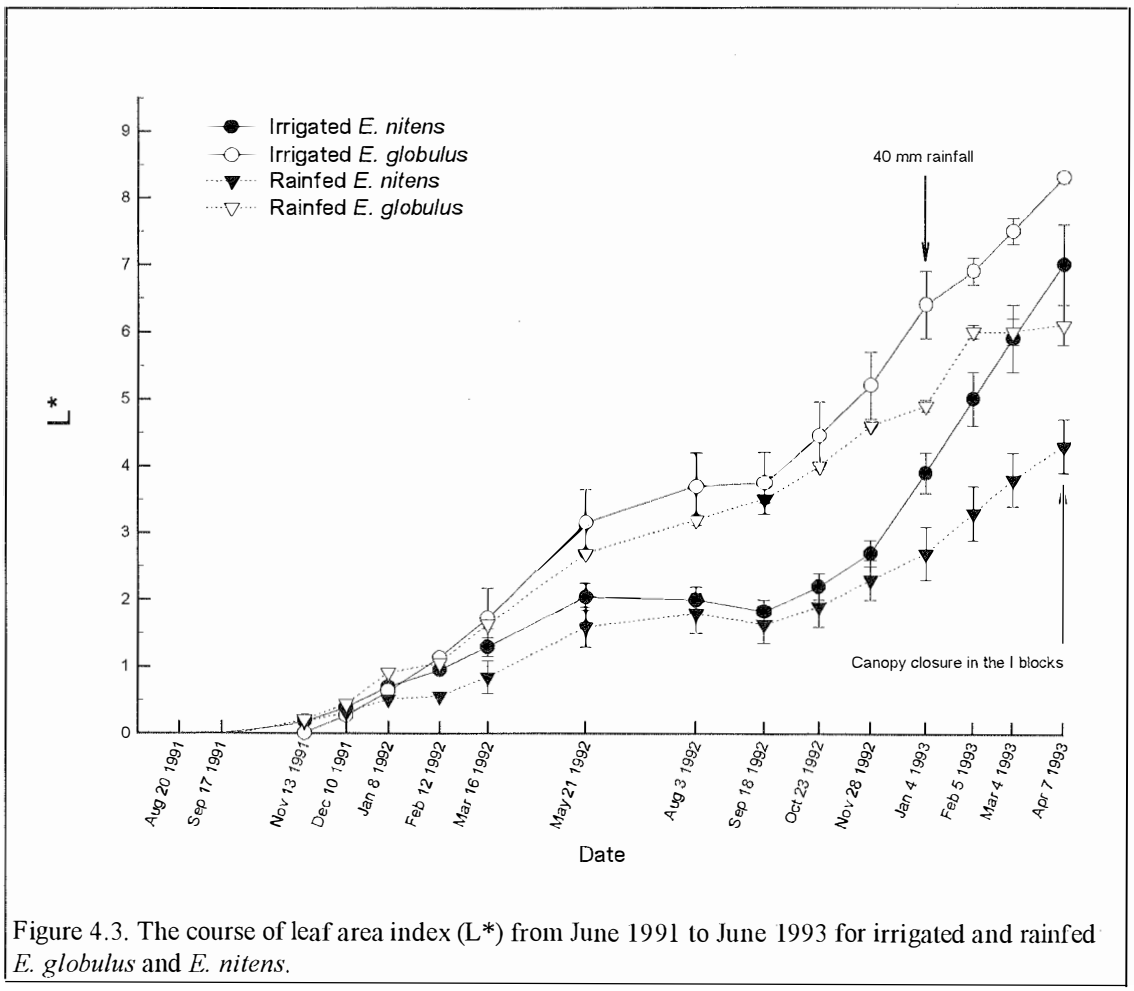

Figure 4.3. The course of leaf area index (L*) from June 1991 to June 1993 for irrigated and rainfed *E. globulus* and *E. nitens*.

4.4 Discussion

Throughout the study period *E. globulus* maintained a greater leaf area index than *E. nitens*, regardless of treatment. Moreover, after November 1992, L* was significantly lower in the R than in the I treatment and this effect was, in absolute and relative terms, more pronounced in *E. nitens* than *E. globulus*. These results are consistent with the observation in Chapter 3 that turgor was maintained over a wider range of leaf relative water content in *E. globulus* than *E. nitens* and does not support the hypothesis that traits which confer cold tolerance on *E. nitens* will render it more drought tolerant than *E. globulus*.

Rates of leaf area development were probably sustained in the I treatment at close to maximum throughout the course of the experiment, except in the winter period. Maximum values of L* in the I treatment of *E. globulus* and *E. nitens* were 8.3 and 6.9 respectively, and these were reached within three years of establishment (Table 4.5). The L* of I *E. globulus* at this time was more than double the value of 3.8 reported for a three-year old irrigated and fertilised *E. globulus* plantation in Portugal of roughly equivalent stocking (Gazarini et al. 1990). Mean overbark diameter at breast height was 12.7 cm in the Portuguese stand compared to 9.0 cm in the current study. L* was 3.2 and 2.1 for I *E. globulus* and I *E. nitens*, respectively, at age two years (Table 4.5). At the same age Roberts et al. (1992) reported L* to be 2.2 and 2.4 respectively in *E. teretecornis* Sm. and *E. camaldulensis* Dehnh. planted at much greater density than in the current study. In studies made in stands grown in cool temperate conditions similar to those of the current study, Beadle and Mummery (1989) found that L* of a related provenance of *E. nitens* peaked at approximately 6 at age 4 years while Morris and Wehner (1987) observed a peak L* of 7 for *E. globulus* at age three years in an effluent irrigated plantation in Victoria. There is some indication that *Eucalyptus* plantations achieve higher values of L* in cooler (Beadle and Mummery 1989) compared to warmer (Roberts et al. 1992, Dye and Olbrich 1993) climates. The Beer-Lambert law (Landsberg 1986), assuming an extinction coefficient of 0.5, predicts that 95% of the incident radiation will be intercepted by a canopy with an L* of 6 (eg. *E. nitens*, Beadle and Mummery, 1989), while 77% of radiation will be intercepted by

a canopy with L* of 3.8 (*E. globulus*, Gazarini et al. 1990). In climates at low latitude where radiation is in plentiful supply and temperature is rarely limiting, canopy photosynthesis may be optimised at much lower L* so that carbon allocated to stem compared to leaf biomass is greater than under the cool temperate conditions of the current study. A possible explanation for this is that as mean temperature increases so do rates of respiration. For pines the change in canopy respiration for an increment of L* relative to the change in carbon assimilation has been observed to be greater for slash pine at a warm site than for loblolly pine at a cool site (Ryan et al. 1994). This might, at least in part, be an explanation for the very high leaf area indices observed in climates where potential productivity is relatively lower.

While the values of L* recorded here seem high for *Eucalyptus* species they are not as high as some of the values reported for coniferous species (eg 10.5 for *Picea abies* (L.) Karst, Bolstad and Gower 1990). In natural coniferous stands in western Oregon L* ranged from as high as 18 in coastal *Picea sitchensis* (Bong.) Carr. to 4 in *Pinus ponderosa* Dougl. stands in the Eastern Cascades. Generally L* in mature *Eucalyptus* stands and other broadleaf forests is lower than for coniferous forests (Jarvis and Leverenz 1983, Linder 1985).

After March 1992 L* was lower in the R compared to the I treatment of both species. This effect became significant in November 1992 and remained so thereafter. Studies of the effect of water stress on leaf area development are limited in eucalypts. The most extensive studies were conducted on juvenile leaves of *E. globulus* in Portugal (Metcalfe et al. 1989, 1990, 1991). Leaf initiation and expansion were reduced by water stress in seedlings (Metcalfe et al. 1989) and the size of this reduction was reported to be of the order of 50 percent (Metcalfe et al. 1990). In a split-root experiment Phillips and Riha (1994) observed a similar reduction in total leaf area due to water stress in *E. viminalis* seedlings. Metcalfe et al. (1991) examined the effect of leaf age on the biophysical variables influencing the expansion of plant cells and found that mature leaves had lower cell wall extensibility and higher cell wall yielding threshold (Lockhart 1965) than juvenile

leaves. While no explicit consideration has been given for the influence of available water on leaf area development of eucalypts in the field, a simple linear relationship has been found between a water balance index and L* of coniferous communities in Western Oregon (Grier and Running 1977). The water balance index considered the influence of precipitation, pan evaporation and soil water storage.

During the 1992/93 growing season development of L* in the R *E. nitens* was steady while that in the R *E. globulus* was stepped (Figure 4.3). The notion of a functional equilibrium between A_l/A_s and k_h (Whitehead et al. 1984), together with results presented in Chapters 3, 5 and 6 provide a possible explanation for this pronounced interspecific difference[5]. Assuming that A_l/A_s and l are constant within a stress cycle equation 4.1 simplifies to

$$k_h \propto \frac{Dg_s}{\Delta\Psi} \qquad (4.3)$$

$\Delta\psi$ increased during water stress and this increase was greater in *E. nitens* than *E. globulus* (Chapter 3, Figure 3.4). Chapter 6 considers the effect of soil water deficit on g_s and shows that g_s of both species was significantly reduced, relative to the I treatment, when pre-dawn leaf water potential was below -0.6 MPa. Equation 4.3 anticipates from these changes that in both *E. globulus* and *E. nitens* k_h will be reduced by periods of water stress and that this reduction will be greater in the latter species. Reduced k_h during water stress has been observed in a range of species (eg. Reich and Hinckley 1989, Tyree et al. 1991) and is probably attributable to embolism in the conducting xylem (Sperry and Tyree 1990). During periods of water stress before March 1993 leaf drop was minimal in both *E. globulus* and *E. nitens*. Subsequently litter traps showed that during water stress litter fall was greater in *E. nitens* than *E. globulus* (Beadle and Worledge, unpublished data). This tendency for *E. globulus* to retain foliage during periods of water stress was corroborated by Dutkowski (pers comm) who observed that *E.*

[5] All of the subsequent discussion relies on the assumption that all of the sapwood area was conducting area. It is acknowledged that the proportion of the sapwood which is conducting may change with tree age, season and treatment.

globulus trees in SW Australia died of drought stress before any leaf drop occurred. The difference between the species in leaf retention points to smaller changes in A_l/A_s in *E. globulus* than *E. nitens* between the beginning and end of each stress cycle. In *E.* globulus, in which leaves are not shed in response to water stress, gas exchange, leaf initiation and expansion will only be maximised after rewatering if k_h is restored to pre-stress values so that the evaporative demand of a largely unchanged leaf biomass can be met from the newly available supply of water. The more rapid increase in leaf area development following rewatering of *E. globulus* than *E. nitens* (Figure 4.3) suggests that restoration of k_h occurred more rapidly in the former species. A corollary of this line of argument is that, as long as k_h can be restored after water stress, the maintenance of high A_l/A_s during water stress allows trees to respond rapidly to increased water availability. This appears to be the strategy employed by *E. globulus*.

This argument relies on A_l/A_s being relatively stable in the short term. Absolute values of dA_l/dA_s and the relative influence of species and treatment on them did change between age 2 (1992) and 3 years (1993), but in both years a strong positive correlation between A_l and A_s was evident for both treatments of both species. This is consistent with the pipe model interpretation of plant form (Shinozaki et al. 1964a, b) and gives some confidence in the approach used to estimate L* between these two sampling dates.

The mean value of dA_l/dA_s across species and treatments was significantly greater in 1992 (1.05) than in 1993 (0.56). This may be due to a change in partitioning of dry matter from leaf to stem between ages 2 and 3 years (Beadle and Inions 1990). Beadle and Mummery (1989) also observed a reduction in dA_l/dA_s in *E. nitens* from 0.81 at age 2 to 0.31 at age 3 years. In the current study, dA_l/dA_s at age 3 was 0.47 in the irrigated *E. nitens* compared to 0.31 in the stand studied by Beadle and Mummery (1989) which had similar growth rates. The original planting density in the former (1430 stems ha^{-1}) was much lower than in the latter (2500 stems ha^{-1}) resulting in earlier closure in the denser stand, accumulation of more `disused pipes' (Shinozaki et al. 1964a) at age 3 years than in the current study and a

proportionately greater reduction in dA_l/dA_s. In *Eucalyptus* species a proportion of the sapwood may be allocated to carbohydrate storage rather than water transport (Hillis 1987).

The value of A_l/A_s was greater in *E. globulus* than *E. nitens*. This difference was more apparent, although still not significant, in 1992 than 1993. Several researchers have suggested a strong species dependence of dA_l/dA_s. Significant interspecific differences were reported between *Pseudotsuga menziesii* Mirb. Franco, *Pinus ponderosa* and *Picea abies* (Grier and Waring 1974). Kaufmann and Troendle (1981) observed that dA_l/dA_s ranged from 0.08 for *Populus tremuloides* Michx. to 0.75 for *Abies lasiocarpa* (Hook.) Nutt.. In each of these studies interspecific differences may have been confounded with site variation. Relationships for *Quercus alba* L. and *Q. velutina* Lamarck (Rogers and Hinckley 1979) and *Abies balsamea* (L.) Mill (Marchand 1984) were found to be stable across a range of sites. In contrast Whitehead (1978) found that dA_l/dA_s was different at each of five sites for *Pinus sylvestris* L..

Although the difference between *E. globulus* and *E. nitens* was less apparent at age 3 than at age 2 years, the effect of water stress on dA_l/dA_s was more pronounced in 1993 than 1992. In 1993 the mean dA_l/dA_s across species was 0.48 and 0.65 in the I and R treatments respectively. It has been argued that increasing stand productivity will increase k_h and in turn dA_l/dA_s. This assertion is based on the observation in many studies of a positive correlation between dA_l/dA_s and site index (Brix and Mitchell 1983, Espinosa Bancalari et al. 1987, Coyea and Margolis 1992). Long and Smith (1988) observed that this positive correlation may simply reflect non-linearities in the relationship between A_l and A_s. An apparently contradictory line of argument is that as stand vigour decreases dry matter allocation patterns alter so that stemwood is afforded a lower priority than leaf biomass (Waring et al. 1980, 1981). Shelburne et al. (1993) argued that in *Pinus taeda* dA_l/dA_s was negatively correlated with stand productivity due to increased allocation of dry matter to leaf production than stemwood in lower productivity stands. The higher dA_l/dA_s in the R compared to the I treatment does

not lend unequivocal support to any of these lines of reasoning and suggests that dA_l/dA_s is related to something more fundamental which may or may not be correlated with early growth or stand vigour. Perhaps the most likely explanation for the higher value of dA_l/dA_s in the R than the I treatment is that slower canopy development in the R treatment resulted in greater partitioning of dry matter to leaf area relative to stemwood than in the I treatment at age 3 years.

While it is probable that dA_l/dA_s of the R treatment will eventually approach that of the I treatment it is clear that L* of both species is reduced by water stress and that on an annual time step, this reduction is greater, in absolute and relative terms, in *E. nitens* than *E. globulus*. *E. globulus* achieves greater leaf area development than *E. nitens* under water limited conditions and it does this in bursts following rainfall or rewatering (Figure 4.3). Given that expansive growth is highly sensitive to changes in turgor pressure (Hsiao et al. 1976, Bradford and Hsiao 1982), this finding is consistent with the observation in Chapter 3 that *E. globulus* has a lower bulk elastic modulus and maintains positive turgor over a wider range of tissue water contents than *E. nitens*.

Chapter 5. A model of stomatal and canopy conductance for irrigated *E. globulus* and *E. nitens*

5.1 Introduction

While the mechanisms involved remain the subject of vigorous study and debate, stomatal conductance is reduced by soil and tissue water deficits. The pattern of this reduction is subject to a great deal of interspecific variation as has been shown from studies of deciduous hardwoods (eg. Kaufmann 1979, Reich and Hinckley 1989, Ranney et al. 1991, Ni and Pallardy 1991), conifers (eg. Running 1980, Lu et al. 1995) and eucalypts (eg. Ladiges 1974, Carbon et al. 1981, Attiwill and Clayton-Greene 1984, Colquhoun et al. 1984).

Some evidence suggests that reductions in photosynthesis during moderate drought are largely mediated by stomatal closure (Pereira et al. 1987). While responses to water stress may direct allocation of carbon away from wood production (Waring et al. 1980), it can be argued that stomatal closure is an important cause of productivity losses during periods of drought. In this sense stomatal conductance integrates other plant responses to drought, including any acclimation in leaf water relations, into a single mechanism. Scaling from leaf to canopy conductance integrates transient stomatal responses to the longer term impacts of drought on photosynthetic production and transpiration. These measures also provide a crucial link between growth and water use. Leaf and canopy conductance represent plant responses to a range of environmental factors and as such may yield valuable insights into the adaptive significance of physiological (leaf water relations, Chapter 3) and morphological (leaf area development, chapter 4) responses to soil and plant water status.

Sensible conclusions can only be made about the effect of water stress on stomatal conductance if the behaviour of well watered trees, growing under the same atmospheric conditions, is understood. A second consideration is that leaf level comparisons of the stomatal conductance of the irrigated and rainfed trees used in this study will not completely describe the effect of water stress. Given that the leaf area index, L*, of the rainfed trees was significantly lower than for the irrigated trees throughout the 1992/93 growing season (chapter 4), it can be argued that the relationship between canopy conductance and transpiration will differ for the two treatments. To understand why this might be so it is necessary to consider the assumptions underlying the use of the Penman-Monteith equation (Monteith 1965). When applied at the canopy scale, this equation calculates transpiration (E) as a function of net radiation (R_n), canopy conductance (g_c), boundary layer conductance (g_a), vapour pressure deficit (D), and the coefficients specific heat (c_p) and density (ρ) of air, the psychrometric constant (γ), the latent heat of vaporisation of water (λ) and the slope of the relation between saturated vapour pressure and temperature (Δ):

$$E = \frac{\Delta R_n + c_p \rho D g_a}{\lambda \left[\Delta + \gamma \left(1 + g_a / g_c\right)\right]} \qquad (5.1)$$

Jarvis et al. (1981) described this equation as the '..most useful transpiration model available..', but pointed out that a key assumption was similar distribution of sources of and sinks for heat and water vapour. If this assumption holds, as it does when ambient vapour pressure deficit (D) is imposed over the whole surface, the canopy may be treated as a single layer or 'big leaf' and transpiration calculated as a simple function of vapour pressure deficit and canopy conductance (McNaughton and Jarvis 1983). Forest canopies are aerodynamically rough and in many instances well coupled (Jarvis and McNaughton 1986). In these circumstances, transpiration has been successfully calculated treating the canopy as a single layer (Tan et al. 1978, Dye and Olbrich 1993). If coupling is weak transpiration can be calculated by applying equation 5.1 to smaller elements, usually layers, and summing values for transpiration calculated for the individual elements. This approach has been

successfully applied many times in a range of species, including *E. camaldulensis* and *E. teretecornis* (Roberts et al. 1992). Raupach and Finnigan (1988) discussed the relative merits of single versus multiple layer models and concluded that multiple layer models were appropriate where the forest canopy was the dominant element in the system. Multiple layer models represent an improvement over 'big leaf' models when L* is high as they allow available energy ($\approx R_n$) to be distributed more appropriately through the canopy than in a single layer model. It has been suggested that rather than using multiple layer models it is more appropriate to calculate an 'effective' canopy conductance in single layer energy balance models. In this approach sunlit upper canopy foliage is weighted more heavily than shaded foliage lower in the crown (McNaughton 1994). Three weighting schemes have been proposed by Raupach (1995). It is these considerations that are crucial to a proper comparison of irrigated and rainfed stands which may differ significantly in canopy size.

Against this background the current chapter develops a canopy conductance model for irrigated *E. globulus* and *E. nitens*. Stomatal responses to variables fluctuating diurnally (radiation, temperature and vapour pressure deficit) are considered and functions describing responses developed. The model is based on measurements of stomatal conductance made at the leaf level and two approaches to integration over the canopy are considered. In the first canopy conductance (g_c) was calculated as the sum of the individual conductances of three canopy layers corresponding to the upper, middle and lower third of the canopy by depth. In the second approach predicted stomatal conductance of the upper canopy foliage was attenuated down the canopy using a light response function and the Beer-Lambert law (Landsberg 1986) to give a predicted canopy conductance (g_c'). This approach is based on one of the three schemes referred to above (Raupach 1995).

The principal objective was to develop a model of leaf level stomatal conductance which can be developed further in chapter 6 to accommodate the effect of soil water deficit on stomatal conductance of the two species. The hypothesis that stomatal conductance (g_{su}) of leaves in the upper canopy of irrigated trees of both

species may be predicted from total solar radiation (Q) and vapour pressure deficit (D) is tested. Assumptions implicit in the two approaches used to calculate canopy conductance are also considered in the context of relationships amongst canopy conductance, photosynthesis and transpiration. The implications of any differences which emerge between g_c and g_c' for the calculation of transpiration using the Penman-Monteith equation are considered further in chapter 7.

5.2 Materials and Methods

5.2.1 Plant material and soil water status

The same 12 trees for which the pressure-volume curves discussed in chapter 3 were constructed were also the subject of the stomatal conductance study described in this and the next chapter (chapter 6). In the following paragraphs the measurement of both treatments of each species is described. Only data from the irrigated treatment, in which irrigation was scheduled to maintain soil water deficit in a non limiting range, are presented in this chapter. The findings will be used in chapter 6 as a basis for quantifying the effect of water stress on stomatal conductance of *E. globulus* and *E. nitens*.

5.2.2 Measurement of stomatal conductance (g_s)

Scaffolding was erected around each of the four groups of three trees (2 treatments x 2 species) to gain access to their crowns. From each tree one leaf was selected from each of two aspects (East and West) within each of three canopy layers corresponding to the upper, middle and lower third of the crown by depth. Only recently fully expanded foliage was selected. This was usually found in the third or fourth pair of leaves from the branch tip. As the trees grew replacement leaves were selected as necessary. Stomatal conductance was measured on both surfaces (abaxial and adaxial) of all leaves, using a Li-1600 steady state porometer (Li-Cor Inc. Lincoln Nebraska). The porometer was calibrated annually over saturated salt solutions giving known humidity at a standard temperature. Stomatal conductance per unit leaf area (g_s) was calculated as the sum of that measured on the adaxial and abaxial surfaces.

Stomatal conductance was measured with varying regularity from September 1991, six weeks prior to commencement of irrigation, to May 1993. In March 1994 an additional three days measurements were made in the irrigated *E. globulus* only. The frequency of measurement was dictated by conditions and spaced to cover the range of soil water deficits experienced by the rainfed treatment. Measurement was most intensive during the growing seasons (October to April) of 1991/92 and 1992/93. Measurement usually started at first light and continued till mid to late afternoon. Where possible at least four full sets of data were collected for both treatments of each species. On five occasions five data sets were collected. It was not always possible to complete a full diurnal course of measurements. If conditions became changeable measurement was aborted. Incomplete diurnal courses of data were not analysed with respect to treatment and species effects but were included in model development.

5.2.3 Leaf area index

In chapter 4 leaf area index (L*) was calculated for the whole canopy and individual layers using allometric equations based on annual destructive sampling. Calculation of L* for both treatments of both species on g_s measurement days was by linear interpolation between the estimates of L* presented in Figure 4.3.

5.2.4 Data analysis

5.2.4a Interspecific and spatial variation

As already indicated, only results for the irrigated treatment are presented in this chapter. The GENSTAT ANOVA procedure (Genstat 5 Committee 1988), which assumes a normal distribution, was used to analyse each set of stomatal conductance data (2 species x 3 trees x 6 leaves = 36 leaves) using the following single factor model.

$$g_{s,ij} = \mu + S_i + e_{ij}$$

where $g_{s,ij}$ was the stomatal conductance of j^{th} leaf from the i^{th} species, μ was the sample mean, S_i, and e_{ij} species and residual variance.

Similarly, within each plot the GENSTAT ANOVA procedure was used to test for the effect of layer and aspect on stomatal conductance. This time the data was analysed as factorial with respect to layer (L) and aspect (A)

$$g_{s,ijk} = \mu + L_i + A_j + LA_{ij} + e_{ijk}$$

Only data from 1000 to 1700 h Australian Eastern Standard Time were analysed in this way as early in the morning changes in stomatal conductance were rapid and the time lag between measurement of species and treatments might have led to differences which were due to changes in atmospheric conditions rather than species or treatment effects.

5.2.4b Model development

In the first instance a model was developed to predict stomatal conductance of leaves in the upper canopy layer (g_{su}). Predicted values were then scaled up to an estimate of canopy conductance (g_c') using a modified version of the approach described by Raupach (1995) and Kelliher et al. (1995). This approach and some assumptions implicit in it were examined using data collected for individual canopy layers. Canopy conductance (g_c') predicted in this way was compared with observed values (g_c) calculated as the sum of observed conductances of individual canopy layers (Equation 5.2):

$$g_c = \sum_{i=1}^{i=3} L^*_i \, g_{si} \qquad (5.2)$$

where L^*_i and g_{si} were observed leaf area index and mean stomatal conductance of the i^{th} canopy layer. Hereafter g_c and g_c' will, respectively, be referred to as 'calculated' and 'predicted' canopy conductance.

5.3 Results

5.3.1 Variation in stomatal conductance

5.3.1a Layer within species

Prior to December 1, 1992, stomatal conductance (g_s) was occasionally, but not consistently, affected by canopy layer. At this time L* was 5.2 and 2.7 in *E. globulus* and *E. nitens* respectively (chapter 4). Subsequently g_s was significantly affected by canopy layer in *E. globulus*, while in *E. nitens* this effect was not apparent until after January 7 1993 when L* was 3.9.

The pattern differed markedly between the species. In *E. globulus* g_s of the upper (g_{su}) and middle (g_{sm}) canopy layers was similar while that of the lower layer (g_{sl}) was usually significantly less than g_{su} or g_{sm}. In *E. nitens* g_{sm} and g_{sl} were similar, while g_{su} was significantly greater than g_{sm} or g_{sl} . These patterns of attenuation were evident on days of high (eg. January 19, 1993, maximum D=3.25 kPa, Figure 5.1a and 5.1c) and low vapour pressure deficit (eg. January 22, 1993, maximum D=1.25 kPa, Figure 5.1b and 5.1d).

5.3.1b Aspect within species (data not shown)

In both species g_s was usually greatest in the eastern half of the tree in the morning and in the western half after midday. This is an entirely unsurprising result but does highlight the importance of having each aspect equally represented.

5.3.1c Species

From June to September 1992 stomatal conductance (g_s) was significantly greater in *E. nitens* than *E. globulus*. At other times of the year, from November to May of 1991/92 and 1992/93, g_s was occasionally significantly higher in one or other of *E. globulus* or *E. nitens* but no consistent pattern was observed. Consequently data for both species were pooled for model development.

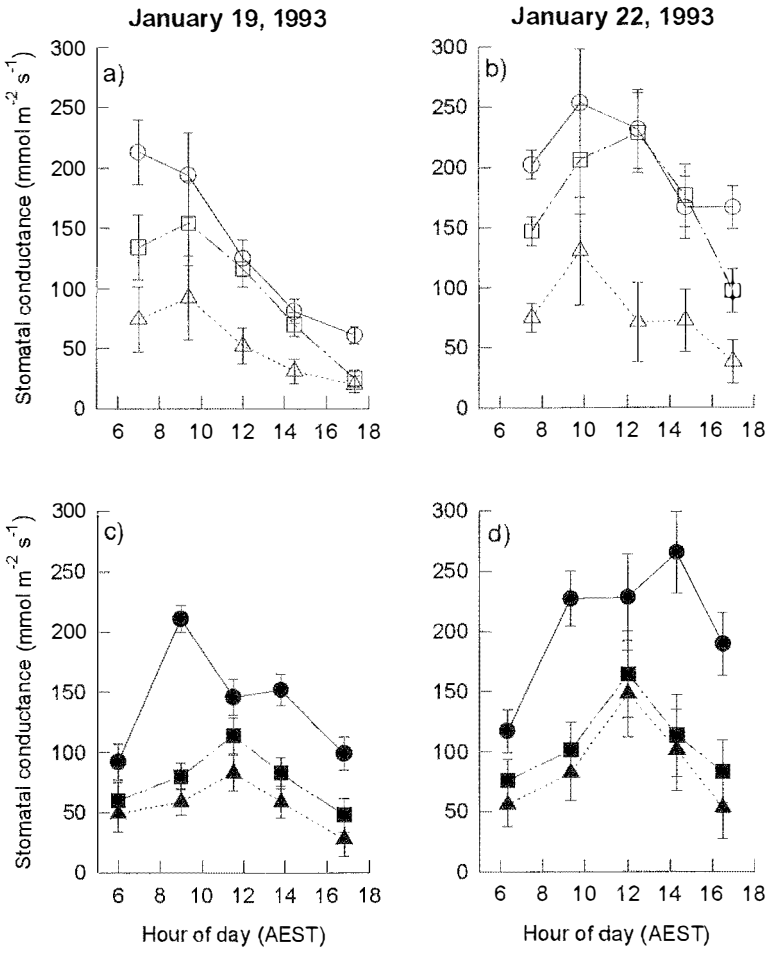

Figure 5.1. Diurnal course of stomatal conductance for the upper (circles), middle (squares) and lower (triangles) canopy layers of irrigated *Eucalyptus globulus* on a) January 19, 1993, when maximum vapour pressure deficit, D, was 3.25 kPa and b) January 22, 1993, when maximum D was 1.25 kPa and c) and d) *E. nitens* on the same two dates respectively (± s.e.).

5.3.1d Diurnal

For *E. globulus*, stomatal conductance of upper canopy foliage (g_{su}) usually increased to a peak mid-morning and declined thereafter (eg. Figure 5.1b). For *E. nitens* g_{su} often peaked at midday or later (Figure 5.1d). When D was high, such as occurred on January 19, 1993, g_{su} of both species peaked earlier in the day (Figure 5.1a and 5.1c) Under low D a diurnal hysteresis was evident when g_{su} was plotted against either Q or D (Figure 5.2a and 5.2b respectively). On January 19, 1993, when D reached 3.25 kPa at 1500 h this hysteresis was more evident in the

relationship between g_{su} and Q than D (Figure 5.3a and 5.3b). Under such conditions the diurnal opening response of both species was significantly reduced (Figure 5.1).

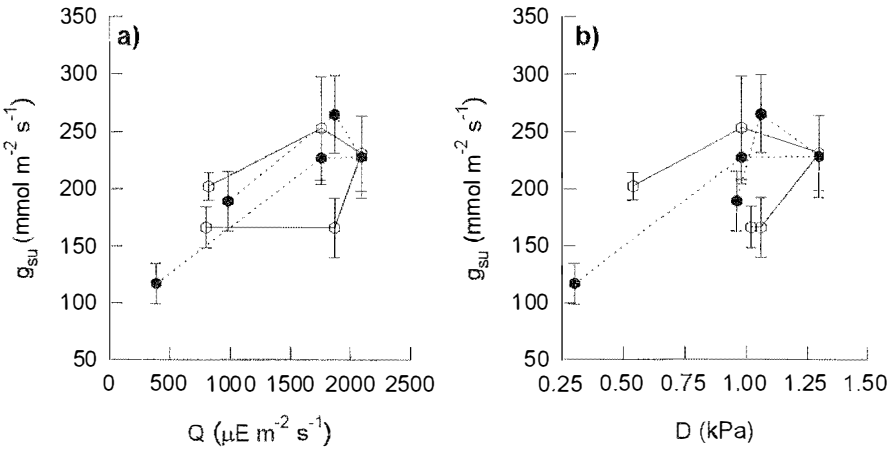

Figure 5.2. Stomatal conductance of the upper canopy layer (g_{su}) as a function of a) total solar radiation (Q) and b) vapour pressure deficit (D) for *E. globulus* (open symbols) and *E. nitens* (closed symbols) on January 22, 1993 (± s.e.).

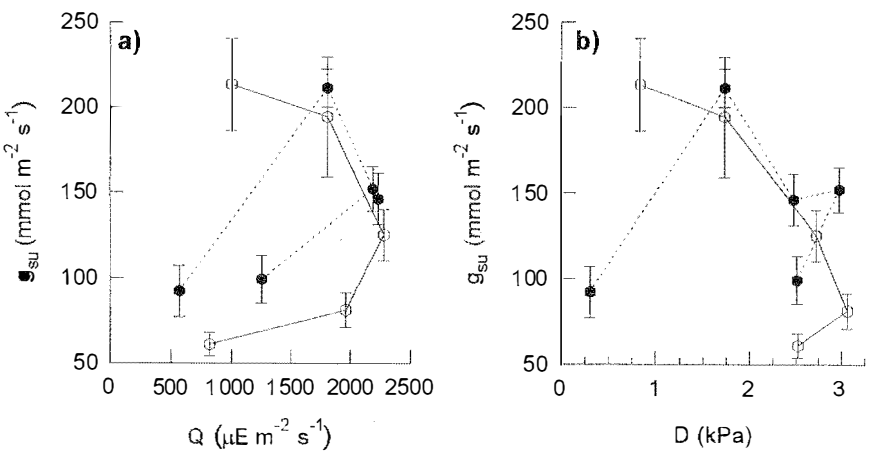

Figure 5.3. Stomatal conductance of the upper canopy layer (g_{su}) as a function of a) total solar radiation (Q) and b) vapour pressure deficit (D) for *E. globulus* (open symbols) and *E. nitens* (closed symbols) on January 19, 1993 (± s.e.).

5.4 Model development

5.4.1 Stomatal conductance of upper foliage

In the first instance a phenomenological model of the form proposed by Jarvis (1976), and based on 1992/93 data, was developed to predict stomatal conductance of the unshaded leaves from the upper canopy (g_{su}). Much of the subsequent presentation and discussion of results is based on data from the upper canopy layer. The rationale for this is twofold. Firstly, the environment to which these leaves are exposed is most closely approximated by data recorded at the weather station. Secondly, light conditions in the upper canopy were independent of stand age and canopy development. If the behaviour of leaves from this layer can be considered independent of stand age then data from the upper foliage of quite small trees might be used to predict the behaviour of a closed canopy.

5.4.1a. Total solar radiation (Q)

A non rectangular hyperbola, of a form used to predict photosynthesis from photosynthetically active radiation (Thornley and Johnson 1990), was fitted by eye to the upper boundary of a plot of normalised g_{su} versus Q (Figure 5.4a). The slope (α) and shape (θ_g) parameters of the relationship (Equation 5.3) were 0.005 and 0.85 respectively.

$$f(Q) = \frac{1}{2\theta_g}\left(\alpha Q + 1 - \sqrt{(\alpha Q + 1)^2 - 4\theta_g \alpha Q}\right) \qquad (5.3)$$

5.4.1b. Air Temperature (T)

Using the same approach a line was also fitted to the upper boundary of a plot of normalised g_{su} against temperature. The equation (5.4) used was of the form described by Jarvis (1976) where T_o was the temperature at maximum conductance and T_l and T_h the lower and upper ends of the temperature range for which a positive stomatal conductance was predicted. The upper boundary of the plot of g_{su} versus T was rather broken and so the parameters of this relationship were taken

from Ogink-Hendriks (1995). T_l, T_o and T_h were assigned values of 0, 17 and 38°C (Figure 5.4b).

$$\left.\begin{aligned} & f(T) = b(T - T_l)(T_h - T)^c \\ \text{where} \quad & c = \frac{(T_h - T_o)}{(T_o - T_l)} \quad \text{and} \quad b = \frac{1}{(T_o - T_l)(T_h - T_o)^c} \end{aligned}\right\} \qquad (5.4)$$

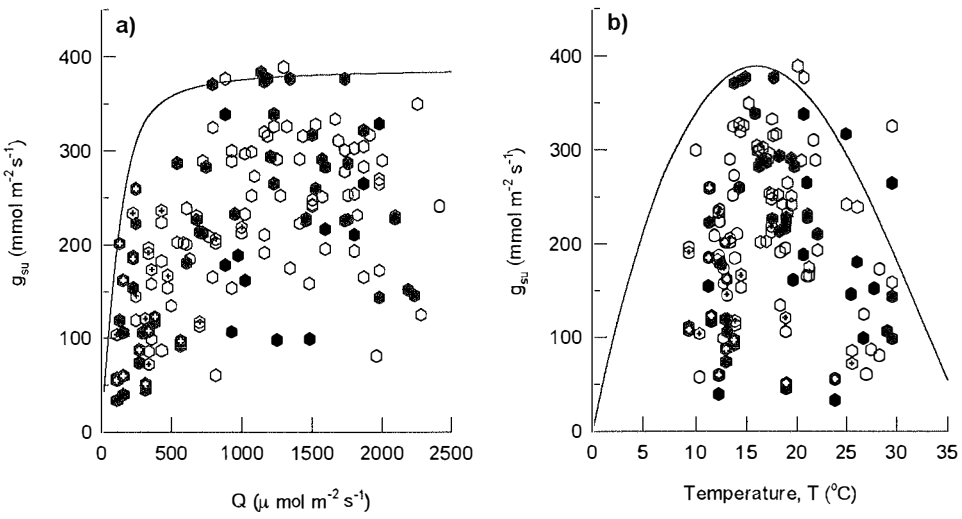

Figure 5.4 Stomatal conductance of upper canopy foliage as a function of a) total solar radiation (Q) and b) air temperature (T) for *E. globulus* (open symbols) and *E. nitens* (closed symbols). The functions f(Q) and f(T), scaled to a maximum of 389 mmol m^{-2} s^{-1}, are also shown. Crosses indicate data recorded less than 1.5 hours after sunrise.

5.4.1c. Vapour pressure deficit (D)

The raw stomatal conductance data for the upper canopy was adjusted using equation 5.5 to give $g_{su,i}'$, a variable from which the influence of Q and T was removed.

$$g_{su,i}' = \frac{g_{su}}{f(Q)f(T)} \qquad (5.5)$$

The subscript i is used here to indicate that the data are for irrigated trees and is included to distinguish $g_{su,i}'$ from a similar variable which will be calculated for rainfed trees in chapter 6. When $g_{su,i}'$ was plotted against D no clear relationship was evident. However when some early morning data was excluded the relationship between $g_{su,i}'$ and D improved (Figure 5.5). An exponential decay function was fitted to a plot of $g_{su,i}'$ against D using the non-linear curve fit routine in SigmaPlot which uses the Marquardt-Levenberg algorithm (Marquardt 1963) to minimise the residual sum of squares. The maximum value of r^2 for this relationship (0.70) was obtained when data recorded less than 1.5 hours after sunrise was excluded. (Figure 5.5). This relationship was normalised to predict a value of 1 when D was 0.2 kPa, the lowest value represented in the data set (Equation 5.6).

$$f(D) = \frac{442e^{-0.63D}}{390} \qquad (5.6)$$

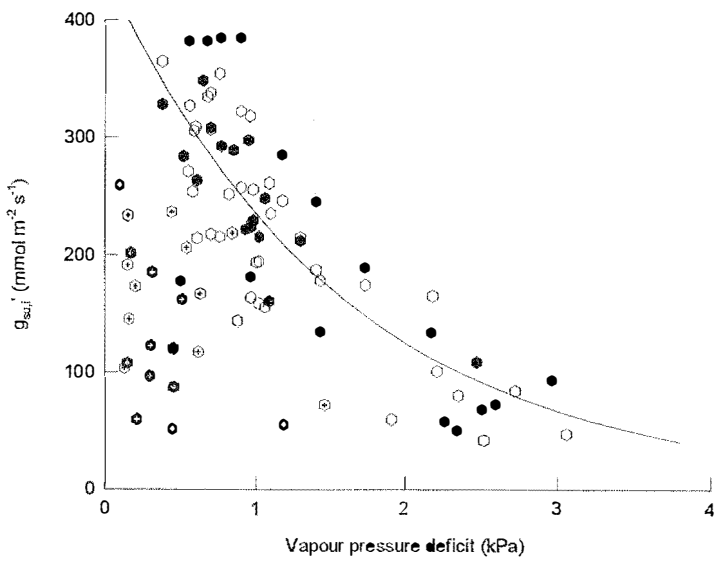

Figure 5.5. $g_{su,i}'$ as a function of vapour pressure deficit (D) for *E. globulus* (open symbols) and *E. nitens* (closed symbols). Data measured less than one and a half hours after sunrise are shown with crosses. The function shown (equation 5.6) was fitted to data measured at least one and a half hours after sunrise (without crosses).

It follows from this that 70 percent of variation in g_{su} of *E. globulus* and *E. nitens* may be explained by equation 5.7.

$$g_{su} = g_{su,max} f(Q)f(T)f(D) \quad (5.7)$$

When predicted g_{su} was fitted to observed values by linear regression the intercept and slope were 74 mmol m^{-2} s^{-1} and 0.7 respectively, so that equation 5.7 overestimated low and underestimated higher values of g_{su} (Figure 5.6a).
If the temperature function, f(T), was not fitted the proportion of variation in g_{su} explained by the model decreased from 70 to 48% (Figure 5.6).

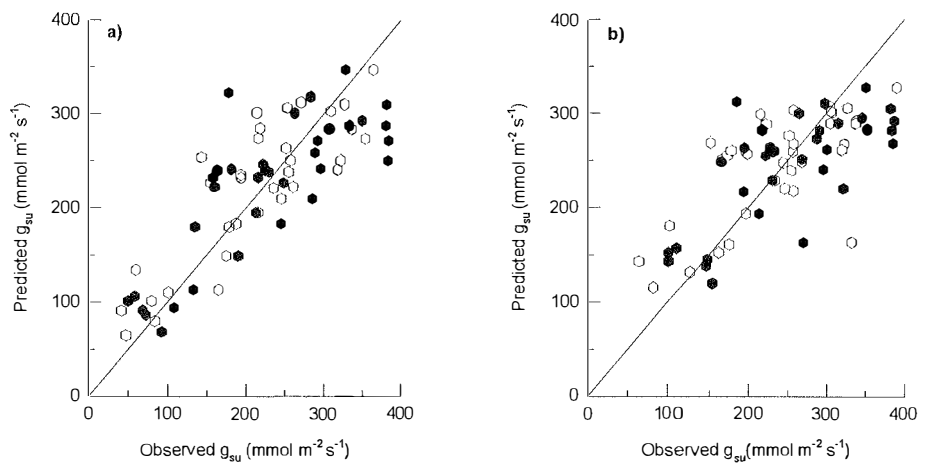

Figure 5.6. Predicted versus observed stomatal conductance for the upper canopy of *E. globulus* (open symbols) and *E. nitens* (closed symbols). a) including f(T) in the model and b) excluding f(T) from the model. The solid lines are 1:1.

When the same fitting procedures were undertaken with 1991/92 data there was no evidence of any change, between years, in the form of f(Q) or f(T). However, because the correlation between g_{su}' and D was poor in 1991/92 this dataset was ultimately excluded from further model development. With the exception of four points for *E. nitens* maximum stomatal conductance of the upper canopy layer ($g_{su,max}$), was approximately 400 mmol m^{-2} s^{-1} in 1991/92, as it was in 1992/93.

5.4.2 Canopy conductance

Dye and Olbrich (1993) predicted canopy stomatal conductance from a relationship derived by linear regression of calculated canopy conductance (g_c), (using equation 5.2 in a four layer configuration), on g_{su}. Since the parameters of the relationships between calculated g_c and g_{su} change with leaf area index, and as such are likely to be site and species dependent, a second approach to predicting canopy conductance (g_c') was considered. The value of f(Q) at a point in the canopy below a given cumulative leaf area index ξ may be calculated as $f(Q_\xi)$ (Kelliher et al. 1995, Raupach 1995), where Q_ξ is the downward flux of radiation at that point in the canopy, which may in turn be calculated using the Beer-Lambert law (Landsberg 1986, Equation 5.8). The Beer-Lambert law attenuates radiation incident at the top of the canopy (Q_0) as an exponential decay function of ξ.

$$Q_\xi = Q_0 e^{-k\,\xi} \tag{5.8}$$

In the current study an extinction coefficient, k, of 0.5 was used. This was the same as that used by Dye (1987) in *E. grandis* Hill ex. Maiden and slightly greater than the value of 0.4 used by Roberts and Rosier (1993) in *E. camaldulensis* and *E. teretecornis*. Replacing f(Q) in equation 5.7 with the integral of f(Q) over the canopy gives equation 5.9 for estimating canopy conductance of a stand with a leaf area index of L*:

$$g_c' = g_{su,max} f(D) f(T) \int_0^{L^*} f(Q_\xi) d\xi \tag{5.9}$$

where it is assumed that:

- The foliage is distributed uniformly throughout the canopy (a requirement of Beers law).
- The values of f(D) and f(T) are unaffected by canopy depth.
- Leaves throughout the canopy have the same maximum stomatal conductance as those of the upper layer (ie. leaves at the bottom of the canopy, if exposed to maximum Q, will return a value for f(Q) of 1).

- The parameters, α, and θ_g, of f(Q) are constant throughout the canopy.

No data was collected which would enable testing of the first assumption. The latter three are now examined:

i). Parameters of f(T) and f(D) are constant

When leaf level stomatal conductance data for the middle (g_{sm}) and lower (g_{sl}) canopy layers was plotted against T there was no evidence that values for T_o, T_l or T_h differed between canopy layers.

f(D) was calculated for the lower canopy layer using equation 5.5 and substituting g_{sl} for g_{su} and replacing f(Q) with $f(Q_\xi)$. Q_ξ was calculated using equation 5.8 assuming that measurement leaves were below a cumulative leaf area index (ξ) equal to the total leaf area index of the upper two layers. f(D) for the upper and lower canopy layer were then compared using a t-test for paired data. For *E. globulus* the value of f(D) calculated in this way was significantly greater in the lower than the upper canopy layer ($p=0.04$). In *E. nitens* there was no effect of canopy position on f(D) ($p=0.88$). This process was repeated to compare f(D) of the upper and middle layers and no significant difference between layers was found in either species. It seems that, at least for *E. nitens*, f(D) is unaffected by canopy position. That is to say, the proportional reduction of g_s by D measured at the weather station was the same throughout the canopy. In *E. globulus* this was not the case. Given that this effect was only just significant beneath a cumulative leaf area index of between 6 and 8 it was decided not to complicate the model by integrating f(D) with respect to ξ.

ii). Constant $g_{s,max}$

In order to explore the relationship between $g_{s,max}$ and cumulative leaf area index (ξ), data collected over the 1992/93 growing season for the irrigated *E. globulus* was divided into subsets on the basis of L* (only data for L* greater than 4 were included). The maximum stomatal conductance at the bottom of the canopy ($g_{sl,max}$) in each subset was regressed on the median L* for the subsets. It was assumed that L* calculated in this way equated to ξ for foliage from the lower canopy. Since

very limited data were available for *E. nitens* where L* was in this range, $g_{s,max}$ measured at four points in another *E. nitens* canopy using an ADC portable gas exchange system with an external light source was regressed on ξ, determined by destructive sampling for the same points in the canopy (Pinkard, unpublished data). Neither the intercepts nor the slopes of relationships between $g_{s,max}$ and ξ differed significantly between species (Equations 5.10 and 5.11, Figure 5.7). However, since the patterns of attenuation down the canopy are known to differ for the species (Figure 5.1) separate relationships were retained in the model.

$$g_{s,max}(\xi) = 399(1-0.073\xi) \quad E.\ globulus \tag{5.10}$$

$$g_{s,max}(\xi) = 399(1-0.100\xi) \quad E.\ nitens \tag{5.11}$$

For both species r^2=0.95 and n=4.

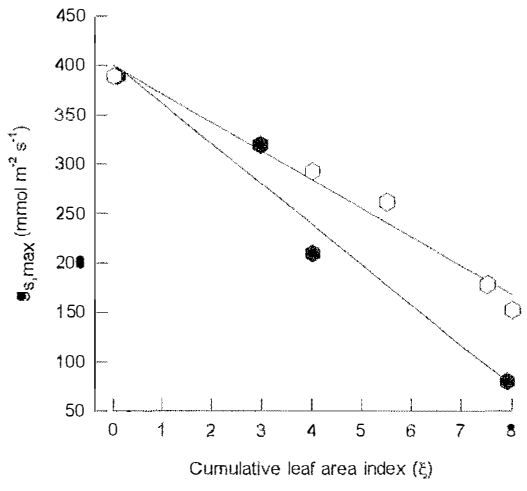

Figure 5.7. Maximum stomatal conductance ($g_{s,max}$) as a function of cumulative leaf area index (ξ) for *E. globulus* (open symbols) and *E. nitens* (closed symbols). Data for *E. nitens* from Pinkard (unpublished).

iii) *Parameters of f(Q) are constant*

If the parameters of f(Q) are constant down the canopy, as assumed by equation 5.9, then when plotted against Q_ξ calculated using equation 5.8, g_{sm} and g_{sl} should fit neatly under f(Q) scaled to maximum g_{su} of 389 mmol m^{-2} s^{-1}. This was the case for g_{sm} (Figure 5.8a) but not for g_{sl} which increased much more rapidly than f(Q) (Figure 5.8b). This suggests that α is positively, but not linearly related to ξ. This assumption is only violated in the bottom third of the canopy. Given the relatively minor contribution of this part of the canopy it is unnecessary to further complicate the model by introducing a dependence of α and θ_g on ξ.

After examination of all the assumptions of equation 5.9 the model becomes:

$$g_c' = f(D)f(T)\int_0^{L^*} g_{s,max}(\xi)f(Q_\xi)d\xi \qquad (5.12)$$

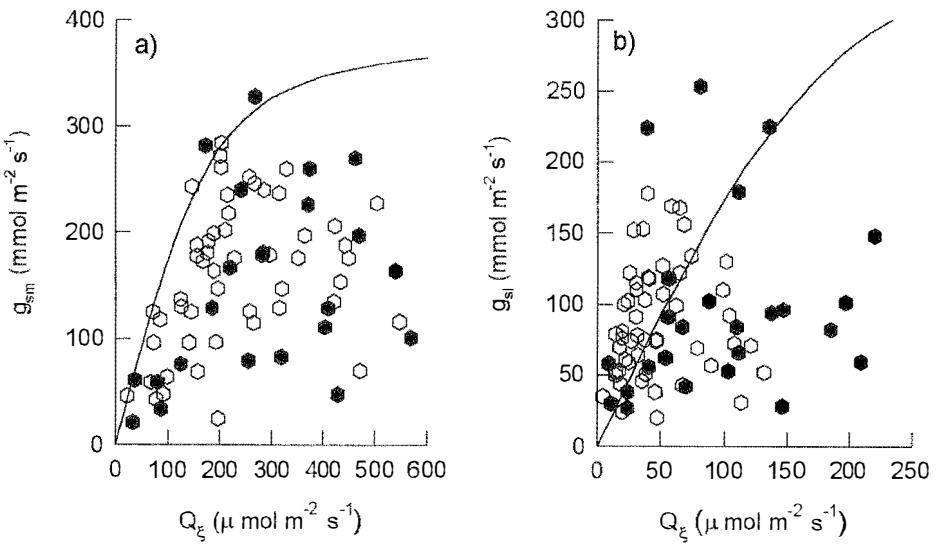

Figure 5.8. Stomatal conductance of a) the middle (g_{sm}) and b) the lower (g_{sl}) canopy layer as a function of $f(Q_\xi)$ calculated from the Beer-Lambert law. For *E. globulus* (open symbols) and *E. nitens* (closed symbols).

5.4.3 Model performance at the canopy scale

5.4.3a Sensitivity analyses

Equation 5.12 predicts maximum canopy conductance when Q, D and T are 2280 μmol m^{-2} s^{-1}, 0.2 kPa and 17°C and when L* is 8.3 and 7.6 for *E. globulus* and *E. nitens* respectively. Under these conditions maximum g_c' predicted for *E. globulus* and *E. nitens* is 1583 and 1410 mmol m^{-2} s^{-1} (Figure 5.9) . To test the sensitivity of the model to the input variables Q, D, T and L* they were varied from their optimal value one at a time. Each was shifted over a range representative of conditions commonly experienced at the site. Over these ranges g_c' was more sensitive to D than to any of the other variables (Table 5.1).

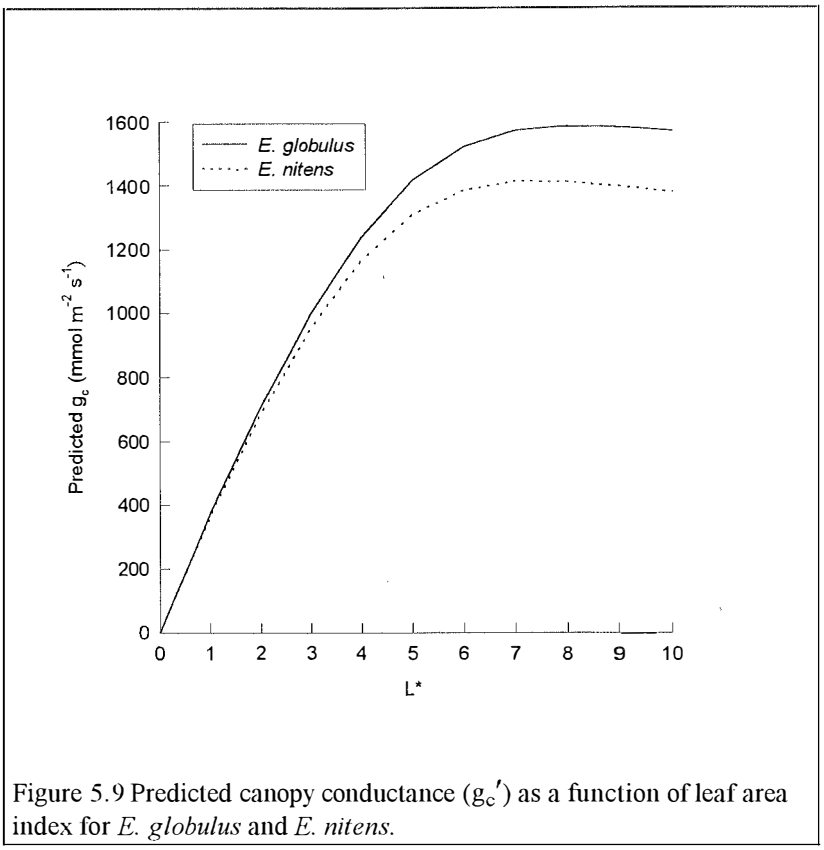

Figure 5.9 Predicted canopy conductance (g_c') as a function of leaf area index for *E. globulus* and *E. nitens*.

With each of these variables set at the optimum value, the sensitivity of g_c' to the parameters of f(Q), f(D) and $g_{s,max}(\xi)$ was also tested. The parameters of f(T) were not considered since this function was not a very important determinant of g_{su}

(Table 5.1). Predicted g_c' was most sensitive to the slope of $g_{s,max}$ (ξ): it was not very sensitive to θ_g or to α above the values chosen (Figure 5.10).

Table 5.1. Percent reduction in predicted canopy conductance of *E. globulus* and *E. nitens* when quantum flux density (Q), air temperature (T), vapour pressure deficit (D) and leaf area index (L*) were varied over commonly observed ranges.

Variable	Range	Percentage reduction in g_c'	
		E. globulus	*E. nitens*
Q (μmol m^{-2} s^{-1})	2280-1000	22	20
Q (μmol m^{-2} s^{-1})	2280-500	43	41
T (°C)	17-27	6	6
T (°C)	17-12	6	6
D (kPa)	0.2-1.4	53	53
L*	8-3.5	22	17

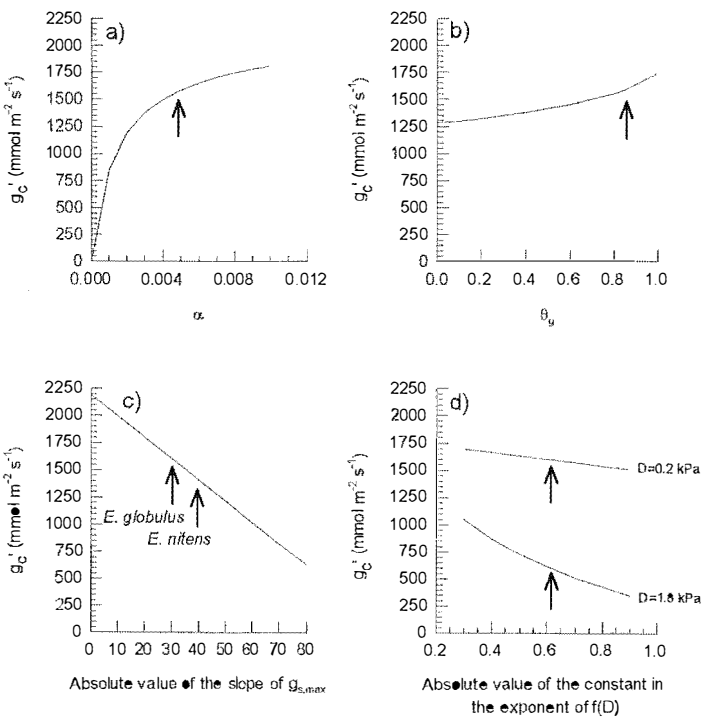

Figure 5.10 Predicted canopy conductance (g_c') as a function of a) α, b) θ_g, c) the slope of f(ξ) and d) the absolute value of the constant in the exponent of f(D). Arrows indicate the values arrived at by analysis of data from the current study.

5.4.3b Predicted values, equation 5.2 versus 5.12

When leaf area index (L*) was less than 6, g_c' predicted by equation 5.12 was a reasonable reflection of the diurnal course of g_c calculated with equation 5.2. This was true for both species. For example on December 1, 1992, when L* was 5.2 and 2.7 in *E. globulus* and *E. nitens* respectively, equation 5.12 slightly underestimated peak values of g_c calculated with equation 5.2 for both species and overestimated it late in the afternoon (Figure 5.11a). There was some evidence that on days of high vapour pressure deficit equation 5.12 underestimated afternoon values of g_c. When leaf area index was greater than 6 maximum g_c was seriously underestimated by equation 5.12. On January 22, 1993, when L* of *E. globulus* and *E. nitens* was 6.9 and 5.0 respectively, equation 5.12 underestimated the maximum g_c of *E. globulus* by 22% but predicted the maximum g_c of *E. nitens* exactly (Figure 5.11b).

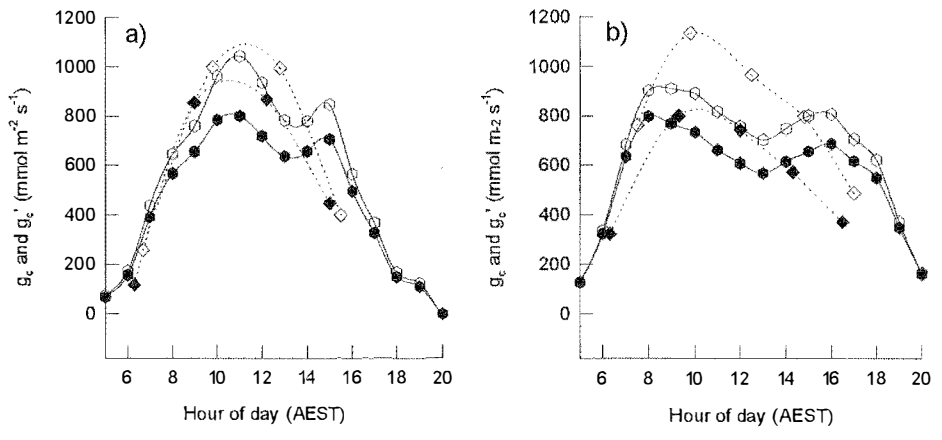

Figure 5.11 Diurnal course of predicted (g_c', solid lines) and calculated canopy conductance (g_c, dotted line) for *E. globulus* (open symbols) and *E. nitens* (closed symbols) on a) December 1, 1992, and b) January 22, 1993.

When values for canopy conductance calculated from equations 5.2 (g_c) and 5.12 (g_c') were integrated over each of 8 measurement days in 1992/93 the effect of L* on the relationship between g_c' and g_c was clearly evident. When points

corresponding to L* greater than or equal to 6 were excluded daily totals of predicted g_c' explained 79% of variation in daily totals of calculated g_c. When data for L* ≥ 6 were included the proportion of variation explained decreased to 67% (Figure 5.12).

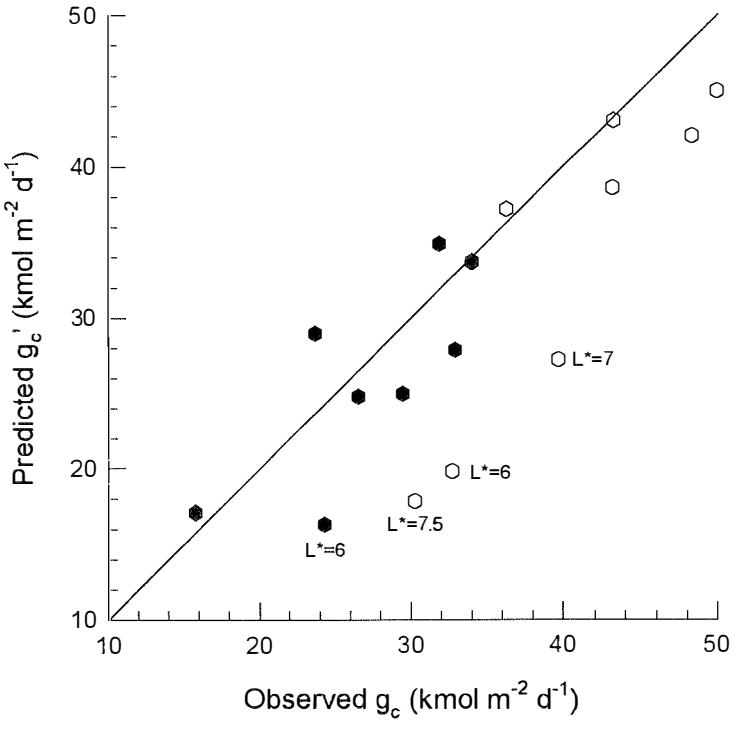

Figure 5.12 Predicted versus calculated daily canopy conductance for *E. globulus* (open symbols) and *E. nitens* (closed symbols). Points corresponding to days when leaf area index (L*) was greater than or equal to 6 are labelled.

5.5 Discussion

Under well watered conditions the stomatal behaviour of well lit, upper canopy foliage was essentially the same for *E. globulus* and *E. nitens*. Perhaps more importantly, the maximum observed stomatal conductance for this foliage was approximately 400 mmol m^{-2} s^{-1} in the 2nd, 3rd and 4th growing season. This suggests that maximum stomatal conductance of young trees may be used as a basis for predicting stomatal conductance and canopy conductance up to and beyond canopy closure. Application of this result to the estimation of canopy conductance, and ultimately transpiration, requires development or application of an appropriate canopy integration scheme. This chapter is essentially in two parts, a phenomenological model of upper canopy conductance and a scheme for integrating predicted values over the canopy. Both parts, and the implications and the assumptions implicit in them, are now discussed.

At the leaf level, the model requires a single plant parameter, the maximum stomatal conductance of upper canopy foliage ($g_{su,max}$). The stability of this parameter across juvenile foliage measured at age 1 year to adult foliage measured at age 3.5 years (canopy closure) is very important as it makes parameterisation comparatively easy. Reported values of $g_{su,max}$ vary considerably between species. In the current study they were greater for both species (400 mmol m^{-2} s^{-1}) than for *E. grandis* (≈320 mmol m^{-2} s^{-1}, Dye and Olbrich 1993) and an order of magnitude greater than the value incorporated in Forest BGC, a general model developed for coniferous species (0.0015 ms^{-1} ≈ 60 mmol m^{-2} s^{-1} at 20°C, Running and Coughlan 1988). By contrast the values of $g_{su,max}$ observed in southern India for *E. camaldulensis* (750 mmol m^{-2} s^{-1}) and *E. teretecornis* (500 mmol m^{-2} s^{-1}, Roberts and Rosier 1993) were greater than those observed here.

Maximum stomatal conductance of upper canopy foliage may vary substantially with site quality and silvicultural practices although little evidence is available to support this assertion directly. However, a substantial body of literature reports a positive correlation between foliar nitrogen concentration and light saturated leaf photosynthesis (DeJong 1982, Evans 1989, Leuning et al. 1991). If the

optimisation principles of stomatal function (Bierhuizen and Slatyer 1965, Cowan and Farquhar 1977, Wong et al. 1978, 1979, 1985a, b, c) hold then $g_{su,max}$ will be correlated with maximum photosynthesis and therefore leaf N concentration. These principles were applied by Leuning et al. (1992) in the array model MAESTRO (Wang and Jarvis 1990), using different values of maximum stomatal conductance for fertilised (500 mmol m^{-2} s^{-1}) and unfertilised *E. grandis* (250 mmol m^{-2} s^{-1}). The value of $g_{su,max}$ reported here reflects the behaviour of foliage which is not limited either by available nitrogen or water and as such represents an expected value for fertilised *E. globulus* and *E. nitens*.

The starting value, $g_{su,max}$, was modified by three functions in a phenomenological model which explained 70% of the variation in stomatal conductance of upper canopy foliage (g_{su}) when measurements made less than 1.5 hours after sunrise were excluded. Use of this phenomenological approach requires confidence in the basic assumption that the upper boundary of scatterplots of the response variate, g_{su}, against explanatory variables, in this case Q and T, represent the unlimited responses to those variables. The calculation of f(D) and subsequent non-linear regression on D rely for their veracity on this assumption. Webb (1972) argued that, for biological data, boundary-line analysis was suitable where the mechanism of the response was understood or the general form was well known. Hall (1982) discussed the merits of phenomenological models of g_s relative to models based on multiple linear and non-linear regression (Hinckley et al. 1975, Pallardy and Kozlowski 1979), and models predicting stomatal conductance as an empirical function of carbon assimilation (Ball 1987, Ball et al. 1987, Leuning 1990). Multiple regression techniques have proved of limited value for building models from stomatal conductance data collected in the field. Indeed, McCaughey and Iacobelli (1994) stated that equations developed by multiple linear and non-linear regression were 'equally poor' for explaining variation in stomatal conductance in a Northern American deciduous forest. Models based on a linear relationship between g_s and carbon assimilation (A) require measurement or estimation of humidity and carbon dioxide concentration at the leaf surface. These variables are difficult to obtain routinely, limiting the applicability of such models in the context

of forest management. Moreover the assumption that A may be used as an independent variable to predict stomatal conductance is erroneous (Aphalo and Jarvis 1993). Leuning (1995) has now adapted this model to solve for A and g_s simultaneously and assigned parameters for *E. grandis*. The simple phenomenological approach adopted here accounted for 70 % of the variation in g_{su} in irrigated trees. This provides a sound basis for quantifying the effect of water stress on g_{su} , the principal objective of this study.

At the leaf level this model strongly resembles similar phenomenological models developed for *E. grandis* (Dye and Olbrich 1993) and *Pinus sylvestris* (Stewart 1988). Both of these models used a rectangular hyperbola to describe stomatal responses to light. This functional form has been used elsewhere (Jarvis 1976, Hinckley et al. 1978, Grace et al. 1982, Ogink-Hendriks 1995, Taconet et al. 1995) and is a special case (θ_g=0) of the non-rectangular hyperbola used in the current study. Thornley and Johnson (1990) recommended use of a non-rectangular hyperbola to describe the response of photosynthesis to light since some biological meaning may be attached to the parameters α and θ. If, at the leaf level, the optimisation principle of Bierhuizen and Slatyer (1965) and Cowan and Farquhar (1977) applies, then it is reasonable to argue that the stomatal response to light will have a similar functional form to the response of photosynthesis to light. It is also noted that the maximum value of f(Q) used by Dye and Olbrich (1993) was 1.05. In common with Dye and Olbrich (1993), when θ_g was set at 0 in this study it was not possible to encompass all the data without setting the maximum value of f(Q) greater than one. This provides further evidence that θ_g is greater than zero for *E. globulus* and *E. nitens*. The value of θ_g used (0.85) suggests a strong dependence of g_s on α at low irradiance (ie. a near linear increase in g_s).

Prior to 1.5 hours after sunrise equation 5.7 significantly overestimated g_{su} (Figure 5.5). This data covers a range of irradiances up to 500 μmol m^{-2} s^{-1} when D was less than 0.75 kPa (Figure 5.4). A possible explanation is that stomatal opening in response to increasing irradiance after a dark period significantly lagged behind photosynthesis (Whitehead and Teskey 1995). If this is the case it suggests that

stomatal response to changing irradiance in *E. globulus* and *E. nitens* is indirect and related to changes in CO_2 concentration in the substomatal cavity which are in turn due to fluctuations in the rate of photosynthesis.

In the current study the variation in observed g_{su} explained by the model increased from 48 to 70% when f(T) was included in the calculation of f(D). The functional form of the relationship used was that suggested by Jarvis (1976). This relationship has been used elsewhere (Stewart 1988, Gash et al. 1989). The temperature optimum was subject to some uncertainty in this study but sensitivity analysis showed that g_s and g_c' are less sensitive to changes in T than to either Q or D. In a study designed to investigate the response of photosynthesis to temperature (Battaglia et al. 1996) g_s was observed to decrease above 25°C and below 10-15°C in summer and autumn. This response was more pronounced in *E. nitens* than in *E. globulus*. Across a range of temperatures from 5°C to 35°C the intercellular CO_2 concentration remained constant in both species which suggests that stomatal response to temperature was also indirect. Battaglia et al. (1996) worked on the same site and with the same trees as in the current study and there is nothing in their results to suggest that the parameters chosen for f(T) are inappropriate. Dye and Olbrich (1993) did not include a temperature function in their model.

Within the range of conditions under which positive rates of photosynthesis are expected predicted stomatal conductance was more sensitive to D than to either Q or T (Table 5.1). The slope parameter of f(D) (-0.63) was much greater than that reported for *E. grandis* during the summer (-0.30) (Dye and Olbrich 1993). This resulted in a 50 and 90% reduction of g_{su} at D of 1.1 and 3.7 kPa in this study compared to D of 2.3 and 7.7 kPa in the latter study. Ogink-Hendriks (1995) and Taconet et al. (1995) used similar exponential decay functions to describe stomatal responses to D while Stewart (1988) used a stepped linear function. As yet no evidence of a physiological sensor in leaves for saturation deficit or absolute humidity has been produced (Monteith 1995a). Mott and Parkhurst (1991) used a mixture of air and helox to vary the water vapour concentration difference between the leaf and air at the leaf surface independently of transpiration rate, thereby

demonstrating that stomata responded to the rate of water loss rather than to vapour pressure deficit (D). Many subsequent studies have supported this observation (eg. Aphalo and Jarvis 1991) and re-analysis of several data sets has illustrated that curvilinear relationships between g_s and D may be reinterpreted as relationships between g_s and transpiration (Monteith 1995b). Dewar (1995) suggested that the rate of transpiration may be sensed via changes in total water potential gradients between guard and adjacent epidermal cells. Transpiration was not estimated independently of g_s or D in the current study so the relationship between g_s and transpiration may only be incorporated indirectly as f(D). The relationship used and its slope parameter suggests that g_{su} of *E. globulus* and *E. nitens* is quite sensitive to the rate of water loss at the leaf surface, ie. that steep gradients of water potential are probably set up between guard and epidermal cells at relatively low transpiration rates.

In physiological studies of transpiration, canopy conductance has often been calculated as the sum of the conductances of individual canopy elements, usually layers (eg. Dye 1987, Dye and Olbrich 1993, Roberts and Rosier 1993). When canopy conductance is calculated in this way (g_c, using equation 5.2) and by equation 5.12 (predicted g_c') the two approaches should yield different quantities. This will be especially so at high leaf area indices as equation 5.12 will give less weight to lower canopy foliage than equation 5.2. Results from these two approaches are now compared against the background of observed spatial variation in stomatal conductance.

The scheme of Raupach (1995) and Kelliher et al. (1995) was modified slightly and both the light response function and g_{smax} were integrated over the stand leaf area index L* with respect to cumulative leaf area index (ξ). Use of the Beer-Lambert Law to determine Q_ξ (Landsberg 1986) for calculation of $f(Q_\xi)$ depends on two important assumptions about the spatial distribution of leaf level stomatal conductance (g_s): that the canopy is horizontally homogeneous and vertically heterogeneous with respect to g_s. Neither *E. globulus* nor *E. nitens* canopies are likely to be horizontally homogeneous since maximum g_s is affected by leaf age

(Field 1987). For estimation of canopy conductance violation of this assumption of horizontal homogeneity will have more serious implications prior to canopy closure when strong horizontal gradients of irradiance are observed. Under such conditions integration of f(Q) with respect to cumulative leaf area index will be a much more complex exercise and use of models such as those developed for rows of trees (Jackson and Palmer 1979, Thornley and Johnson 1990) may be necessary.

When stand leaf area index was greater than 4, g_s was significantly affected by canopy position for both *E. globulus* and *E. nitens* although the pattern of attenuation differed markedly for the two species. In the top half of the canopy there was little attenuation of g_s in *E. globulus* but a marked attenuation in *E. nitens*. In the bottom half of the canopy g_s decreased more dramatically in *E. globulus* than *E. nitens* (Figure 5.1). These patterns are the reverse of what might be expected on the basis of the distribution of leaf area in July 1993 (Chapter 4, Table 4.2), 53% of the leaf area being in the top two thirds of the *E. globulus* canopy compared to 40% for *E. nitens*. It seems reasonable to suggest that this interspecific difference might reflect some intrinsic difference either in the extinction coefficient and/or the distribution of carbon sources (and nitrogen sinks) within the canopy. No data are currently available to either support or refute this hypothesis. Vertical gradients of stomatal conductance have been observed for a range of arboreal species including *Pinus sylvestris* (Beadle et al. 1985b), *Picea sitchensis* (Leverenz et al. 1982), *E. grandis* (Dye and Olbrich 1993), *E. camaldulensis*, *E. teretecornis* (Roberts and Rosier 1993) and *terra firme* rainforest species (Roberts et al. 1990). In *P. sitchensis* g_s was found to decrease with whorl number from the top to the bottom of the canopy. This was true for both current and 1 year old shoots and this reduction was steeper after whorl 4 although radiation flux density decreased most steeply in the upper portion of the canopy (Leverenz et al. 1982). This pattern of attenuation, where the reduction in the top of the canopy is less than in the bottom half is similar to that observed in *E. globulus* but the opposite to that observed in *E. nitens*. In *E. grandis* attenuation of g_s occurred almost linearly with canopy depth (Dye and Olbrich 1993). Attenuation of f(Q) using the Beer-Lambert law predicts that decline in stomatal conductance will be steepest at the top of the

canopy suggesting that its application may be appropriate for *E. nitens* but will underestimate canopy conductance for *E. globulus*. The disparity between species in the way g_s is attenuated was indirectly accommodated by the use of different slopes of the relationship between $g_{s,max}$ and ξ for the two species (equations 5.10 and 5.11).

When integrated over the full day predicted g_c' (equation 5.12) explained 79% of the variation in calculated g_c (equation 5.2) while L* was less than 6. At values of L* greater than 6 predicted g_c' underestimated calculated g_c by as much as 41% or 12.5 kmol m^{-2} d^{-1} (Figure 5.12). Apparently predicted and calculated canopy conductances represent different quantities at high leaf area indices. Calculated values are based on a profile of measured stomatal conductance while predicted values rely on the Beer-Lambert law to generate this profile. Equation 5.12 predicts that, when everything else is optimal, increasing L* from 6 to 8 results in a 4 and 2% increase of g_c in *E. globulus* and *E. nitens* respectively. By contrast, when equation 5.2 is used, the same 33% increase in L* increases g_c by 33%. A possible explanation for this disparity is that violation of the assumption of constant α at high leaf area indices results in equation 5.12 underestimating calculated g_c at high leaf area index.

While equation 5.12 underestimated g_c (calculated by equation 5.2) at high L*, the model used here gives less weighting to shaded than to well-lit foliage. In this way use of equation 5.12 may resolve differences between the distribution of sources of and sinks for heat and water vapour to give a better estimate of transpiration than calculated canopy conductance when used in single layer applications of the Penman-Monteith equation. If it is assumed that stomata will only open when Q_ξ exceeds the light compensation point for photosynthesis then the rate of photosynthesis will be distributed throughout the canopy in a way that is correlated with measured stomatal conductance. If this is true then canopy photosynthesis will be closely correlated with canopy conductance calculated with equation 5.12 (g_c). Thus canopy photosynthesis will be more tightly linked to L* than transpiration. This leads to the conclusion that as leaf area index increases from 6 to 8 water use

efficiency may increase in *E. globulus* and *E. nitens* canopies. If this is the case, then any reduction in canopy conductance (due to stomatal closure or reduction of leaf area index) might reduce water use efficiency at the canopy scale. This will be reconsidered in chapter 6.

Equation 5.7 explained 70% of variation in stomatal conductance for upper canopy foliage of both species. As such this equation provides a good working model for evaluating the stomatal conductance of water limited trees in chapter 6. Equation 5.12 is an empirical canopy conductance model which gives acceptable predictions of canopy conductance up to an L* of 6. At L* > 6 this model underestimated canopy conductance calculated as the sum of the conductances of individual canopy layers. This indicates that as L* increases from 6 to 8, the water use efficiency of *E. globulus* and *E. nitens* may also increase. In chapter 7 the relationship between these two estimates of canopy conductance and transpiration will be considered.

Chapter 6. Quantifying the effect of water stress on stomatal conductance of *Eucalyptus globulus* and *E. nitens* leaves and canopies.

6.1 Introduction

The reduction of stomatal conductance by soil moisture deficit has been demonstrated for a range of deciduous hardwoods (eg. Kaufmann 1979, Reich and Hinckley 1989, Ni and Pallardy 1991, Ranney et al. 1991), conifers (eg. Running 1980, Lu et al. 1995)) and eucalypts (eg. Ladiges 1974, Carbon et al. 1981, Attiwill and Clayton-Greene 1984, Colquhoun et al. 1984), but inclusion of this effect in models of stomatal conductance has been restricted to the deciduous hardwoods (eg. Ogink-Hendriks 1995) and conifers (eg. Stewart 1988, Running and Coughlan 1988, McMurtrie et al. 1990). Calder (1992) indirectly incorporated 'physiological control' as a factor in an empirical model of transpiration by *E. camaldulensis* and *E. teretecornis* in southern India, otherwise no attempt has been made to directly quantify the effect of soil moisture deficit, or a measure thereof, on stomatal conductance in *Eucalyptus* species.

Previous models have quantified the effect of water stress on stomatal conductance as a function of the instantaneous value of a chosen indicator of water stress, often the available water fraction. Not withstanding the apparent success of this approach in *Pinus sylvestris* (Stewart 1988) and *Quercus rubra* L. (Ogink-Hendriks 1995) it seems unlikely that the relationship between stomatal conductance and any given indicator of soil moisture deficit will necessarily remain stable within or between stress cycles. Equation 4.1 (Whitehead et al. 1984) predicts that, in the short term, hydraulic conductivity, k_h, will decrease during water stress. Such a reduction has been observed (eg. Reich and Hinckley 1989) and is probably attributable to embolism in the conducting xylem (Tyree and Sperry 1988). In the longer term,

changes in the dimensions of conducting elements within the xylem during drought (Shepherd 1964, Glerium 1970, Aloni 1987) might also reduce k_h in response to water stress. As drought hardening is often associated with periods of water stress (eg. Clemens and Jones 1978) the relationship between g_s and soil water deficit might also change with successive stress cycles within a growing season. A more appropriate way to quantify the effect of water stress on stomatal conductance may be a cumulative measure of that stress.

The effect of soil drought on stomatal conductance of *Eucalyptus* species has been studied, in the main, in native forests. These studies have been largely ecological and aimed at explaining the distribution of species in terms of soil water availability in the context of a range of atmospheric and edaphic factors (eg. Davidson and Reid 1989). In the current chapter stomatal responses to soil drought are described with a view to determining the relative suitability of *E. globulus* and *E. nitens* for establishment on water limited sites. Essentially the questions being asked are the same as in previous studies, but the inclusion of irrigated controls has enabled separation of the effects of soil water deficit from other factors. In chapter 5 the stomatal conductance of upper canopy foliage of irrigated *E. globulus* and *E. nitens* was described by a single equation (equation 5.7) reflecting the similar behaviour of this foliage in both species. This equation will be used as a starting point to quantify the effect of soil water deficit on stomatal and canopy conductance of the two species. It is hypothesised that *E. nitens,* which has higher relative water content at the turgor loss point than *E. globulus* (see chapter 3), will reduce its stomatal conductance at higher (less negative) pre-dawn water potentials than the latter species. A second hypothesis that pre-dawn water potential, an instantaneous measure of soil water deficit, will be inadequate to describe the effect of water stress on stomatal conductance within a given stress cycle is also tested.

6.2 Materials and Methods

6.2.1 Plant material, water status and treatments

All measurements were made in the physiology plots as described in chapter 5. Throughout the study two indicators of soil water status were measured regularly, soil water deficit (Δw) (derived from Neutron Moisture Meter measurements of soil water content, θ_s, after Honeysett et al. 1992) and pre-dawn leaf water potential (ψ_{max}) measured using the pressure chamber technique (Scholander et al. 1965).

6.2.2 Data analysis

The GENSTAT ANOVA procedure (Genstat 5 Committee 1988), which assumes a normal distribution, was used to analyse each full set of stomatal conductance data (2 species x 2 treatments x 3 trees x 6 leaves = 72 leaves) using the following factorial model

$$g_{s,ijk} = \mu + S_i + W_j + SW_{ij} + e_{ijk}$$

where $g_{s,ijk}$ is the stomatal conductance of k^{th} leaf from the jth treatment and ith species, μ is the sample mean, S_i is species, W_j is treatment, SW_{ij} is interaction and e_{ijk} is residual variance.

Similarly, within each rainfed physiology plot the GENSTAT ANOVA procedure was used to test for the effect of layer and aspect on stomatal conductance. As for the irrigated treatment in chapter 5 these results were analysed as factorial with respect to layer (L) and aspect (A).

$$g_{s,ijk} = \mu + L_i + A_j + LA_{ij} + e_{ijk}$$

The analysis was restricted to data collected after 1000 hrs Australian Eastern Standard Time as early morning changes in stomatal conductance are rapid and the time lag between measurement of species or layers may have led to significant differences between treatment which are due to changes in incident radiation.

6.2.3 Model development

Model development was based on analysis of variance results and a canopy conductance model for irrigated canopies of the same species (chapter 5), the rationale being that the effects of soil water can only be quantified if data for well watered trees under the same conditions is available. For the purposes of model development ψ_{max} (chapter 3) was used as an indicator of soil water status in the rainfed blocks.

6.3 Results

6.3.1 Water stress and species by water stress interactions

During the period over which stomatal conductance was measured, six water stress cycles were experienced by the rainfed (R) treatment. For the purposes of this study a stress cycle was defined as any period during which pre-dawn water potential (ψ_{max}) of the R treatment was significantly lower than in the irrigated (I) treatment. These cycles were described in Table 3.1 (Chapter 3, Leaf water relations). The days for which the full diurnal course of stomatal conductance is available for both treatments of both species are listed in Table 6.1 together with the values of ψ_{max} recorded for the rainfed plots on that day. Results of analyses of variance for the effects of water stress and species by water stress interactions on stomatal conductance (g_s) are also included in Table 6.1.

Between December 1991 and early February 1992 two stress cycles were imposed. During the first cycle, on November 28 and December 11, 1991, a significant species by water stress interaction was evident. This effect was also apparent during the second cycle on February 1, 1992, and was manifested as a greater reduction in g_s of *E. nitens* than *E. globulus* with the onset of water stress (Figure 6.1a, b, and c). Water stress significantly reduced g_s between 1000 and 1700 hours once ψ_{max} was less than -0.5 MPa (Table 6.1).

Table 6.1. Results of analyses of variance for water stress and species by water stress effects on stomatal conductance (g_s). Data are presented by measurement day. If significant, and increasing, water stress was being experienced by the rainfed treatment then rows are shaded pale grey. Unshaded rows represent measurements made in a period following re-watering. The dark grey row represents a day when no water stress had been experienced for 3 months. Significance levels are indicated as NS ($p>0.05$), * ($p<0.05$), ** ($p<0.01$) and *** ($p<0.001$). An effect was recorded as significant if it was observed in at least one data set between 1000 and 1700 hours. $^{+}$ On March 12, 1992 g_s was significantly higher in the R than the I treatment.

Date	ψ_{max} (MPa)	ψ_{max} (MPa)	Significance level	
	E. globulus	*E. nitens*	Water Stress	Species by Water Stress
28 Nov 1991	-0.53	-0.46	NS	*
11 Dec 1991	-0.59	-0.58	***	***
1 Feb 1992	-1.24	-2.01	***	***
21 Feb 1992	-0.30	-0.26	***	***
28 Feb 1992	-0.26	-0.26	***	***
12 Mar 1992	-0.34	-0.32	*** ($^{+}$)	***
22 Oct 1992	-0.33	-0.40	NS	NS
1 Dec 1992	-0.70	-0.68	***	**
8 Dec 1992	-0.88	-0.79	***	***
16 Dec 1992	-1.20	-1.15	***	NS
19 Jan 1993	-0.35	-0.19	NS	***
22 Jan 1993	-0.29	-0.24	NS	*
3 Feb 1993	-0.58	-0.55	*	*
19 Feb 1993	-0.76	-0.76	***	NS
18 Mar 1993	-1.03	-0.97	***	NS
25 Mar 1993	-1.20	-1.15	***	**

Between February 6 and 9, 1992, approximately 125 mm of irrigation was applied to the water stressed blocks, returning them to field capacity. During the following month, three diurnal courses of g_s were measured: on February 21 and 28 and March 12, 1992. On February 21 and 28, 1992, g_s of the I treatment remained significantly greater than that of the R treatment and a significant species by water stress interaction was evident. On March 12, 1992, g_s of the R *E. globulus* was greater than in the I treatment. In contrast g_s of the R *E. nitens* remained low in comparison to the I treatment (Figure 6.2 a, b, c)

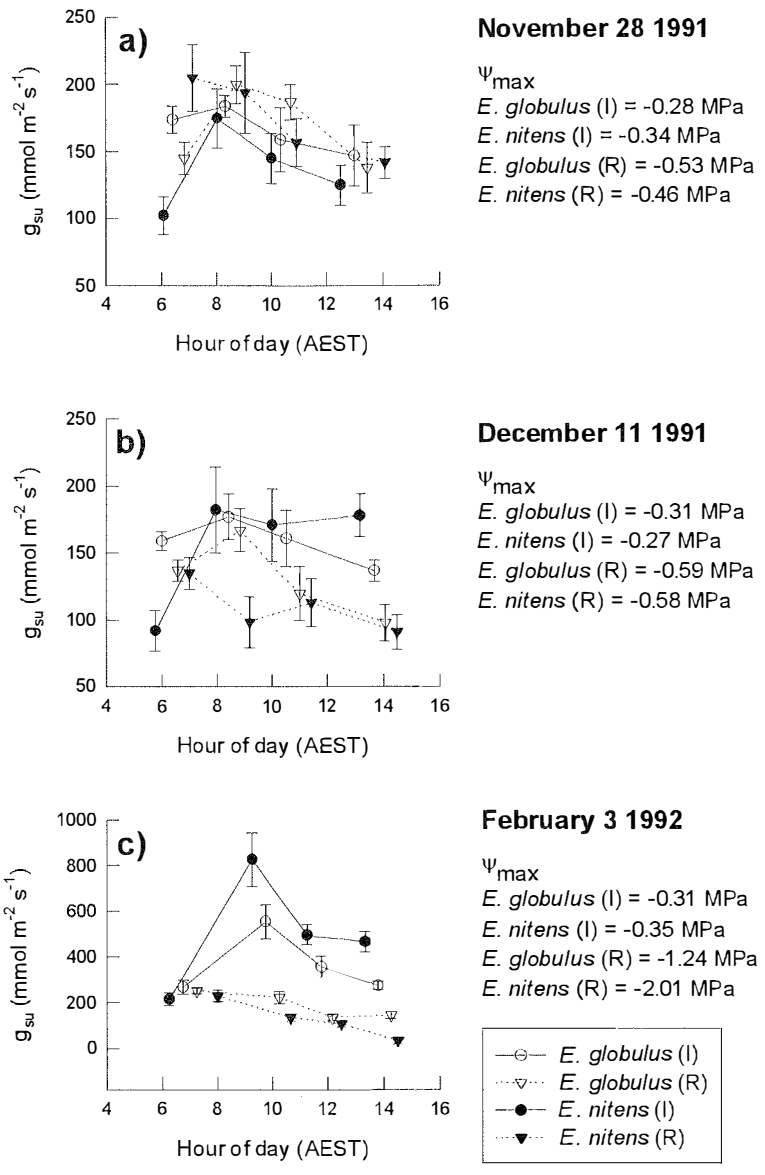

Figure 6.1. Stomatal conductance of the upper canopy layer as a function of time of day for I and R *E. globulus* and *E. nitens* on a) November 28, 1991, b) December 11, 1991, and February 1, 1992.

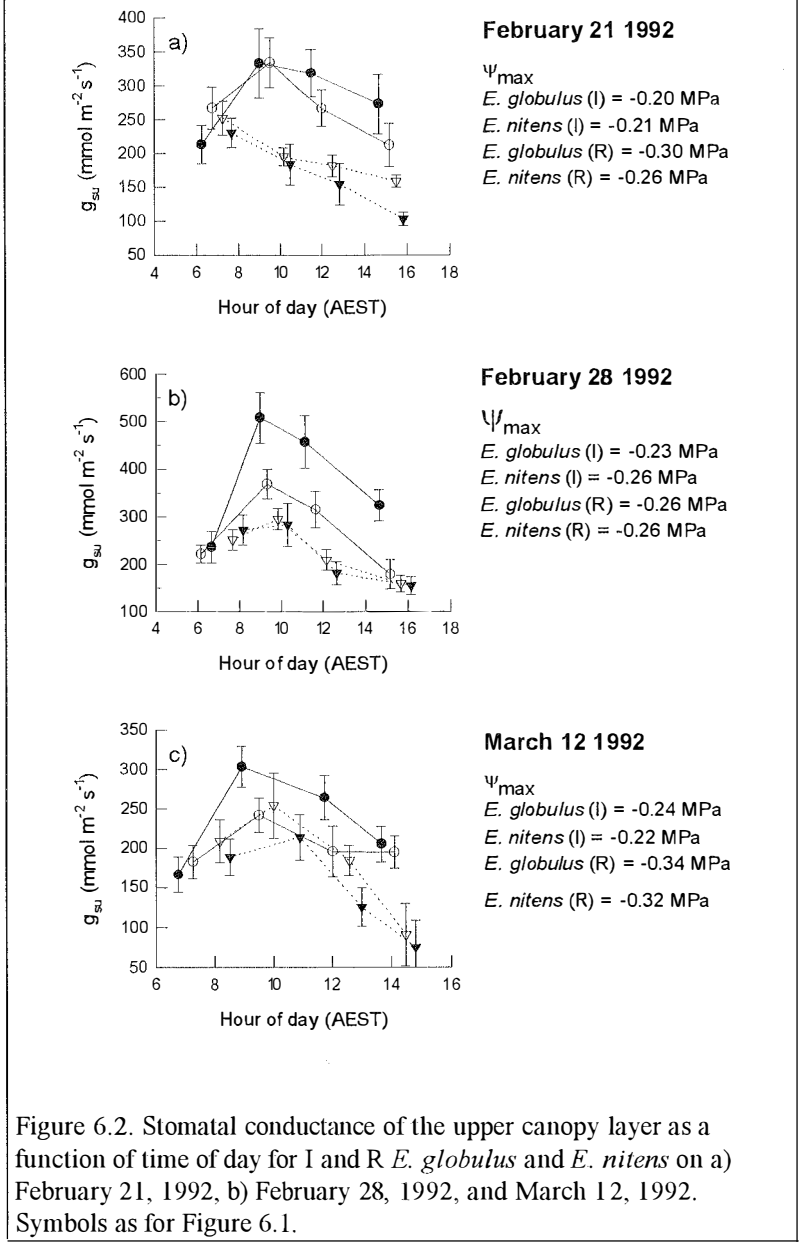

Figure 6.2. Stomatal conductance of the upper canopy layer as a function of time of day for I and R *E. globulus* and *E. nitens* on a) February 21, 1992, b) February 28, 1992, and March 12, 1992. Symbols as for Figure 6.1.

Appreciably more data were available for 1992/93 than 1991/92. The effect of water stress on g_s, however, was substantially similar to that observed in the previous year. In December 1992, during the first stress cycle of that growing season, water stress significantly reduced g_s and this reduction was greater for *E. nitens* than *E. globulus*, again resulting in a significant water stress by species interaction on two of three measurement days (Table 6.1). After re-watering in early January 1993 g_s recovered in the R *E. globulus* to approximately pre-stress levels, but recovery in the R *E. nitens* remained incomplete right up to

commencement of the next stress cycle. In the second and third stress cycle of this season a greater effect of water stress on g_s of *E. nitens* compared to *E. globulus* remained evident as a significant species water stress interaction on February 3 and March 25, 1993 (Table 6.1).

6.3.2 Layer

In May 1993, when measurements finished, L* of rainfed *E. globulus* and *E. nitens* was 5 and 3.7 respectively. Up to this point no consistent effect of canopy layer on g_s was observed in the rainfed plot of either species. This is in contrast to the irrigated plots where canopy position became an important determinant of g_s once leaf area index was greater than 4.5 (Chapter 5).

6.4 Model Development

In this section, observed responses of stomatal conductance to water stress and its alleviation are incorporated into an empirical canopy conductance model developed for irrigated canopies of the same species (Chapter 5).

6.4.1 Stomatal conductance of upper canopy foliage

In Chapter 5 stomatal conductance of well lit upper canopy foliage (g_{su}) was described by equation 5.7 which moderated the maximum stomatal conductance of this foliage, $g_{su,max}$ with f(Q), f(T) and f(D), normalised functions of total solar radiation (Q, μmol m^{-2} s^{-1}), air temperature (T, °C) and vapour pressure deficit (D, kPa) respectively. For irrigated canopies, f(Q) and f(T) were fitted by eye to the upper boundary of normalised plots of g_{su} against Q (equation 5.3) and T (equation 5.4) respectively. The stomatal conductance of upper canopy foliage ($g_{su,i}'$) with any limitation due to irradiance or temperature removed was then calculated using:

$$g_{su,i}' = \frac{g_{su}}{f(Q)f(T)} \qquad (6.1)$$

The corresponding variable, $g_{su,r}'$, for water stressed canopies may be calculated from equation 6.1 using the value of g_{su} for a water stressed canopy.

It is reasonable to suggest that the upper canopy of the I and R trees experience the same atmospheric conditions so that at any given time the ratio of $g_{su,r}'$ to $g_{su,i}'$ should reflect the effect of soil water status. This will include direct effects of soil water status and any interaction of soil water status with vapour pressure deficit. In principle, when the R trees are not experiencing current or residual effects of water stress $g_{su,r}'/ g_{su,i}'$ should equal one. For this important assumption to hold $g_{su,max}$ and the parameters of f(Q) and f(T), which define the limitations due to Q and T, must be the same for irrigated trees and trees subjected to repeated cycles of water stress. Plotting g_{su} of rainfed trees against Q and T for the 1991/92 and 1992/93 growing seasons and superimposing f(Q) and f(T), derived in Chapter 5 for irrigated trees, suggests that this important assumption is reasonable (Figure 6.3 a and b). It is also worth noting that when $g_{su,r}'$, calculated from equation 6.1, was plotted against D, much more residual variation was evident than was the case for $g_{su,i}'$ (Figure 6.3c c/f Figure 5.5). Moreover the upper boundary of this plot was closely approximated by the exponential decay function (equation 5.6) fitted by non linear regression to data for irrigated trees.

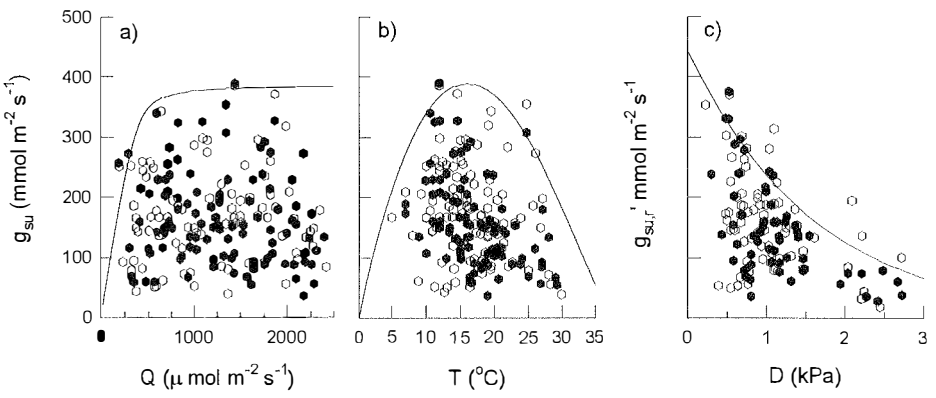

Figure 6.3. Stomatal conductance of the upper canopy of R *E. globulus* and R *E. nitens* as a function of a) total solar radiation (Q) and b) air temperature (T). c) $g_{su,r}'$ calculated for rainfed trees from equation 6.1 as a function of vapour pressure deficit (D) for *E. globulus* and *E. nitens*. All measurements for the 1991/92 and 1992/93 growing seasons are plotted. The lines on a), b) and c) are, respectively, f(Q), f(T) and f(D) derived for irrigated canopies measured under the same range of conditions and scaled to give a maximum conductance of 387 mol m^{-2} s^{-1} (Chapter 5).

6.4.1a Diurnal patterns of $g_{su,r}'/g_{su,i}'$

The ratio of $g_{su,r}'/g_{su,i}'$ was subject to a great deal of diurnal variation on all measurement days in the 1991/92 growing seasons (Figure 6.4 a-f). For example on December 11, 1991 when ψ_{max} of the R treatment of *E. globulus* and of *E. nitens* was, -0.59 and -0.58 Mpa respectively, $g_{su,r}'/g_{su,i}'$ varied from 0.7 to 0.5 for *E. nitens* and 1.0 to 0.7 for *E. globulus* (Figure 6.4b). Later in the same summer, on February 1, 1992, when ψ_{max} was much lower in the R than the I treatment for both species (Table 3.1), the range of values observed for $g_{su,r}'/g_{su,i}'$ varied from 0.6 to 0.4 in *E. globulus* and 0.4 to 0.1 for *E. nitens* (Figure 6.4c). In the recovery period following re-watering, February 21 and 28 and March 12, 1993, $g_{su,r}'/g_{su,i}'$ was significantly higher for *E. globulus* than *E. nitens* (Figure 6.4 d, e and f).

Similar patterns were observed in 1992/93. On December 1 and 8, 1992, when ψ_{max} was between -0.68 and -0.90 MPa for both species, $g_{su,r}'/g_{su,i}'$ varied between 0.9 and 0.5 for *E. globulus* and 0.4 and 0.2 for *E. nitens* (Figure 6.4g and h). After irrigation to field capacity in the first week of January 1993 $g_{su,r}'/g_{su,i}'$ increased more rapidly in *E. globulus* than *E. nitens* and was significantly higher in the former species on January 19 and 22, 1993 (Figure 6.4i and j). During the next stress cycle (cycle 6, Figure 3.1a) on February 19, 1993, and March 18, 1993, a range of values of $g_{su,r}'/g_{su,i}'$ were again observed but the effect of water stress was similar for the two species (Figure 6.4k and l).

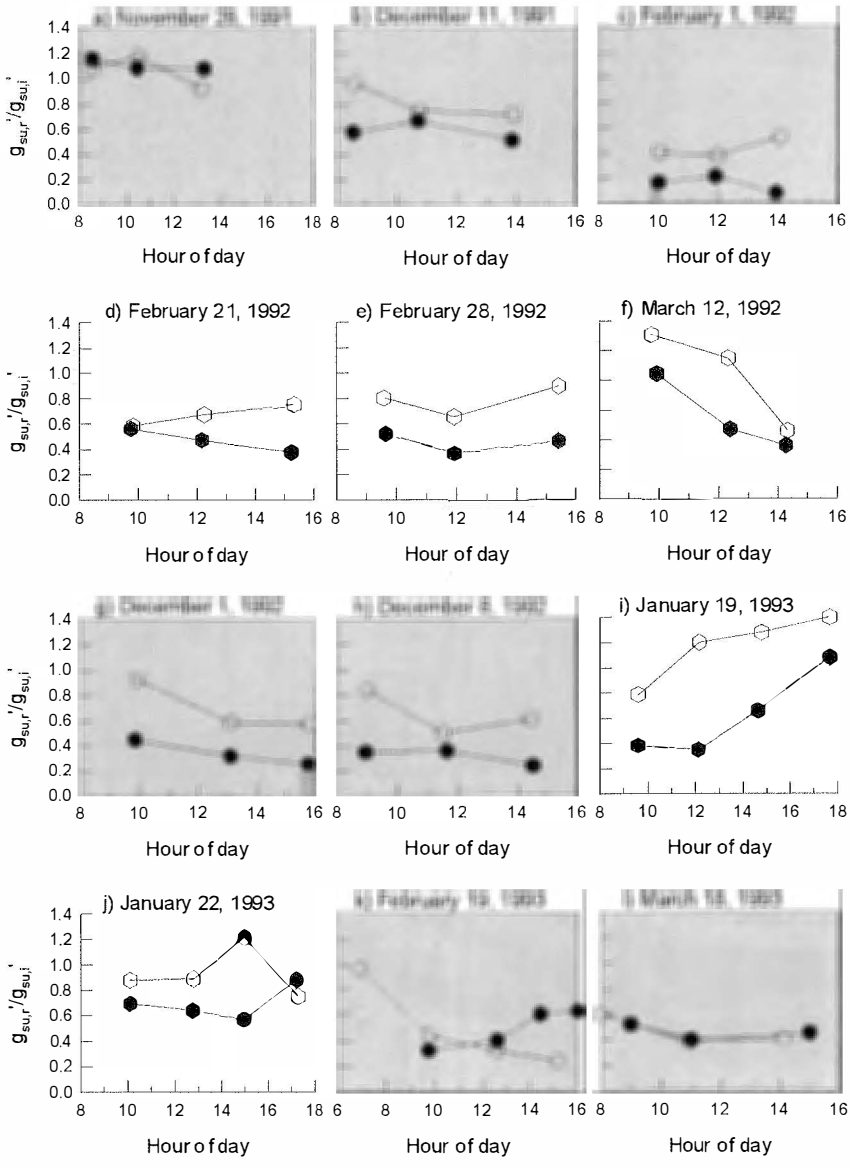

Figure 6.4. Diurnal course of $g_{su,r}'/g_{su,i}'$ for *E. globulus* (open symbols) and *E. nitens* (closed symbols) on a) November 28, 1991, b) December 11, 1991, c) February 1, 1992, d) February 21, 1992, e) February 28, 1992, f) March 12, 1992, g) December 1, 1992, h) December 8, 1992, i) January 19, 1993, j) January 22, 1993, k) February 19, 1993, and l) March 18, 1993. Plots with a grey background are from periods when water stress is increasing and unshaded plots are from recovery periods following rewatering or rainfall.

6.4.1b Ratio of total daily $g_{su,r}'$ to total daily $g_{su,i}'$

The diurnal variation evident in $g_{su,r}'/g_{su,i}'$ indicates that any attempt to characterise the effect of water stress on instantaneous values of g_s measured at different times of the day would be futile. Instead, daily integrals, from sunrise (t_r) to sunset (t_s), of $g_{su,r}'$ and $g_{su,i}'$ were calculated using the trapezoid rule where extrapolation to and from the earliest and latest measurement was done by drawing a straight line to zero conductance at sunrise and sunset respectively. The ratio (f(W)) of total daily $g_{su,r}'$ to total daily $g_{su,i}'$ should reflect the effect of soil water deficit on g_{su} at a daily time step:

$$f(W) = \frac{\int_{t_r}^{t_s} g_{su,r}' \, dt}{\int_{t_r}^{t_s} g_{su,i}' \, dt} \qquad (6.2)$$

f(W) was fitted by linear regression to the absolute value of ψ_{max} for the same day. The resultant relationships for both species were poor. Coefficients of determination (r^2 values) for *E. globulus* and *E. nitens* were 0.46 and 0.30 when data from both growing seasons were included (Figure 6.5a and 6.5b) and improved marginally to 0.47 and 0.50 when only 1992/93 data were analysed (Figure 6.5c and d).

When f(W) was plotted against ψ_{max} for the first stress cycle and recovery period in 1992/93, a pronounced hysteresis was evident in the relationship so that f(W) was greater for a given value of ψ_{max} when ψ_{max} was decreasing than during the subsequent recovery period (Figure 6.6). This hysteresis was also evident for other stress cycles which were followed by a defined recovery period and was consistently more pronounced in *E. nitens* than *E. globulus*.

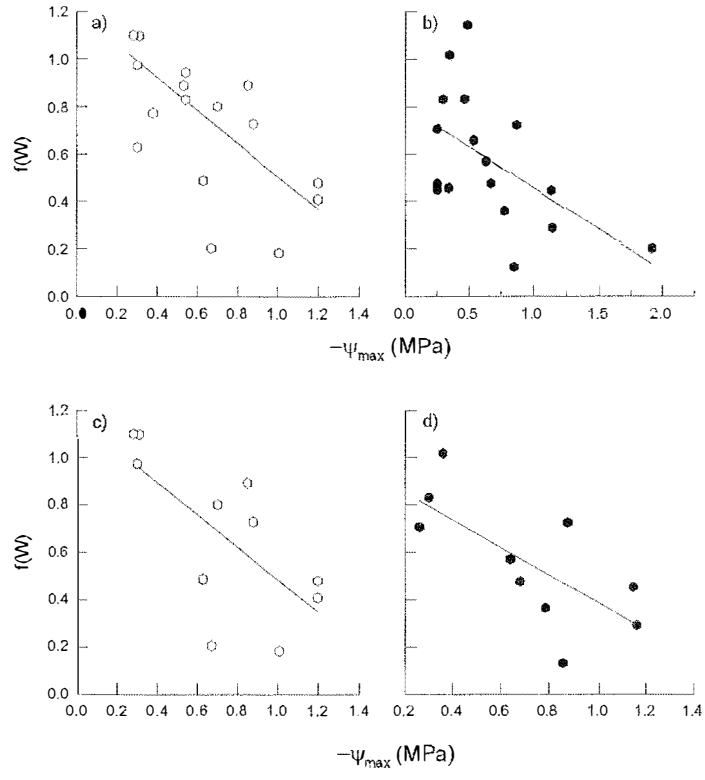

Figure 6.5. f(W) as a function of pre-dawn leaf water potential (ψ_{max}) using a) and b) all data and c) and d) only 1992/93 data for *E. globulus* and *E. nitens* respectively. Lines were fitted by linear regression.

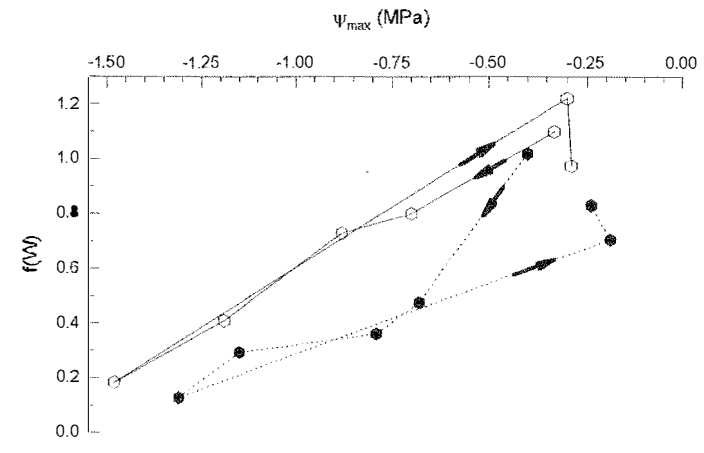

Figure 6.6. f(W) as a function of ψ_{max} for a single stress cycle and recovery period in 1992/93, for *E. globulus* and *E. nitens*. Points are joined in a temporal sequence to illustrate the hysteresis.

To describe the observed hysteresis in the relationship between f(W) and ψ_{max} the cumulative water stress integral (S_ψ) for the previous x days ($S_{\psi x}$) was calculated after Myers (1988) as:

$$S_{\psi x} = \sum_{i=1}^{i=x} \left(|\psi_{max}| - 0.2 \right) \quad (6.3)$$

where ψ_{max} for days between measurements was calculated by linear interpolation. The number of preceding days (x) over which $S_{\psi x}$ was calculated was increased by one day at a time and relationships between f(W) and $S_{\psi x}$ derived by linear regression. When all data were included for *E. globulus* the r^2 value increased to 0.76 when x was 8 (Figure 6.7a) after which increases in r^2 were less than 0.01 for each increment of x. For *E. nitens* 59% of the variation in f(W) was explained by $S_{\psi x}$ when x was 20 (Figure 6.7b).

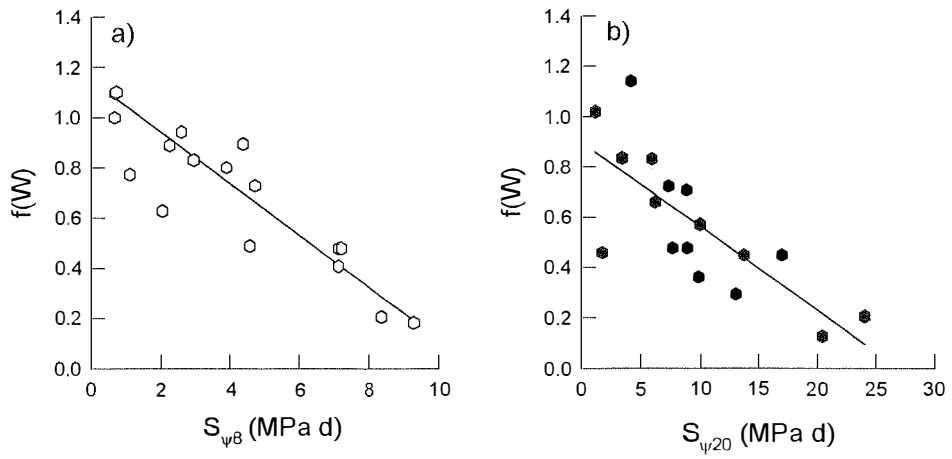

Figure 6.7. f(W) as a function of $S_{\psi x}$ (calculated from equation 6.3) for a) *E. globulus* and b) *E. nitens*, where x was 8 for *E. globulus* and 20 for *E. nitens*.

For *E. nitens* further improvement in the correlation between f(W) and $S_{\psi 20}$ was observed when the weighting of preceding days was reduced linearly until ψ_{max}

measured 20 days before measurement had half the effect of the current ψ_{max} (equation 6.4). No such improvement was achieved by varying the weighting of ψ_{max} in the calculation of $S_{\psi 8}$ for *E. globulus*. Thus for *E. globulus* $S_{\psi 8}$ was calculated with equation 6.3 while equation 6.4 was used to calculate $S_{\psi 20}$ for *E. nitens*.

$$S_{\psi 20} = \sum_{i=1}^{20} \left(\left(1 - 0.025[i-1]\right) \left(\left| \Psi_{\max,i} \right| - 0.2 \right) \right) \qquad (6.4)$$

Weighting $S_{\psi 20}$ in this way for *E. nitens* resulted in a curvilinear relationship between f(W) and $S_{\psi 20}$ to which an exponential decay function was fitted using the non-linear curve fit routine in SigmaPlot (Figure 6.8b, Table 6.2). Similarly an exponential decay function was fitted to the unweighted value of $S_{\psi 8}$ for *E. globulus* (Figure 6.8a). When the entire dataset was included the r^2 values for the resultant functions were 0.73 and 0.75 for *E. globulus* and *E. nitens* respectively. These correlations were even better, 0.90 and 0.86 for *E. globulus* and *E. nitens* respectively, when analysis was restricted to data from the 1992/93 growing season (Figure 6.8, Table 6.2).

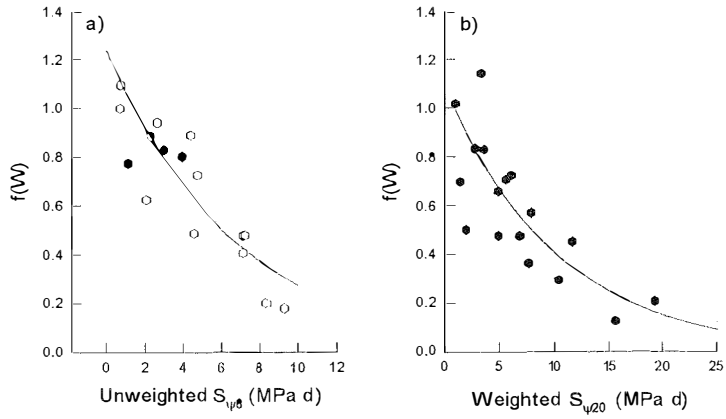

Figure 6.8 f(W) as a function of a) unweighted $S_{\psi 8}$ for *E. globulus* and b) $S_{\psi 20}$ for *E. nitens*

Table 6.2. Relationships for f(W) as a function of the cumulative water stress integral for the preceding x days ($S_{\psi X}$), where x was 8 and 20 for *E. globulus* and *E. nitens* respectively. Relationships for the entire dataset and for only 1992/93 data are included.

Species	Dataset	Relationship	r^2 value
E. globulus	1991-93	$f(W) = 1.24e^{-0.15S_{\psi 8}}$	0.75
E. globulus	1992/93 only	$f(W) = 1.25e^{-0.145S_{\psi 8}}$	0.86
E. nitens	1991-93	$f(W) = 1.095e^{-0.099S_{\psi 20}}$	0.73
E. nitens	1992/93 only	$f(W) = 1.219e^{-0.119S_{\psi 20}}$	0.90

6.4.2 Total daily canopy conductance

If equation 5.12 is integrated with respect to time, from sunrise (t_r) to sunset (t_s), and the result moderated with f(W) calculated using the equations given in table 6.2, total daily canopy conductance (G_c') may be predicted as:

$$G_c' = f(W)\int_{t_r}^{t_s}\left(f(D)f(T)\int_{0}^{L^*} g_{s,max}(\xi)\, f(Q)\,d\xi \right)dt \qquad (6.5)$$

6.4.3 Model performance

As a test of the model, canopy conductance for the I and R treatments of *E. globulus* and *E. nitens* was predicted with equation 6.5 from hourly meteorological data for the period from October 1992 to early February 1993 and values for L* from chapter 4. f(W) was calculated using the relationships for all data in Table 6.2. The ratio of total daily predicted canopy conductance (G_c') for the R treatment to G_c' for the I treatment was calculated and the time course of this ratio plotted together with values for the same ratio for total daily calculated canopy conductance (G_c), where G_c was calculated as the area under the diurnal plot of calculated canopy conductance (g_c) which was in turn derived as in chapter 5 using:

$$g_c = \sum_{i=1}^{i=3} L^*_i\, g_{si} \qquad (6.6)$$

where L_i and g_{si} are , respectively, the leaf area index and mean stomatal conductance of the i^{th} canopy layer. The period selected includes three periods of water stress (cycles 4, 5 and 6, Figure 3.1a) and the recovery periods that separate them. The model characterised the residual effect of water stress (the recovery period) on total daily canopy conductance quite well, especially for *E. nitens* (Figure 6.9). In periods of increasing water stress equation 6.5 tended to underestimate the effect of water stress on canopy conductance calculated as the sum of the conductances of individual layers (equation 6.6).

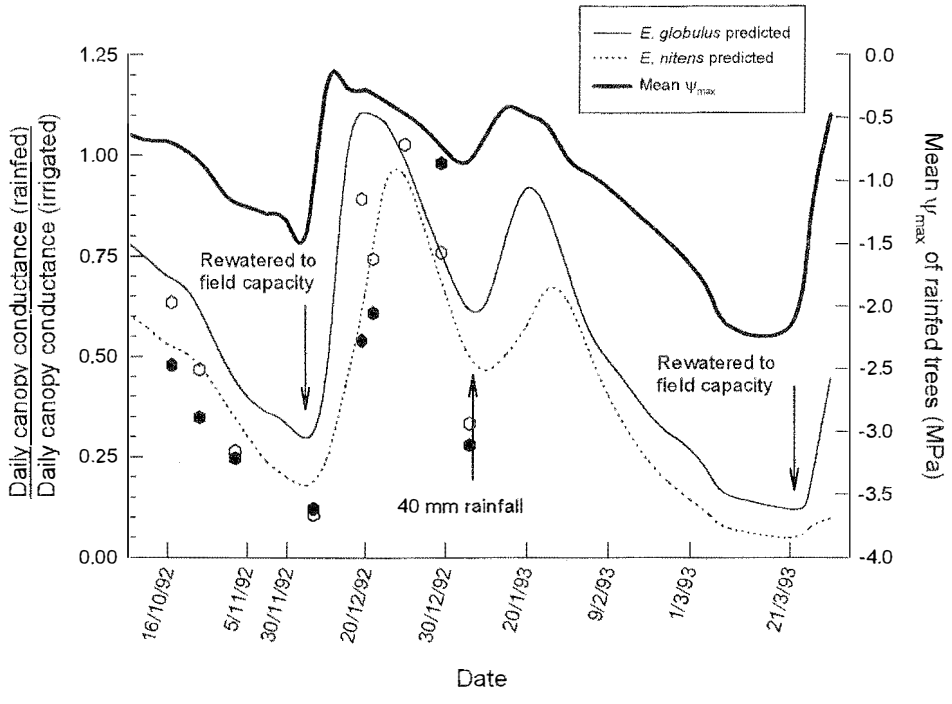

Figure 6.9. Predicted and calculated values of the ratio of total daily canopy conductance of the rainfed canopy to total daily canopy conductance of the irrigated canopy for *E. globulus* (solid line and open symbols) and *E. nitens* (dashed line and closed symbols). The heavy line is a plot of mean ψ_{max} for the same period (October 1992 to April 1993).

6.5 Discussion

Stomatal responses to soil water deficit differed markedly between *E. globulus* and *E. nitens*. Stomatal conductance (g_s) of both species was significantly reduced when pre-dawn leaf water potential (ψ_{max}) reached -0.55 MPa. Below this value of ψ_{max}, g_s was reduced more, relative to the irrigated treatment, in *E. nitens* than *E. globulus*. After rewatering, g_s of the R *E. nitens* remained depressed for up to three weeks, long after ψ_{max} had recovered to greater than -0.4 MPa. In contrast g_s of the R *E. globulus* recovered to be greater than that of the I trees within one week of rewatering. By expressing changes in stomatal conductance due to water stress in terms of those observed in irrigated control trees under the same atmospheric conditions (Chapter 5), these interspecific differences could be described by two simple equations (Table 6.2) which predicted the effect of soil water status on g_s as a function of a cumulative water stress integral (S_ψ) (Myers 1988). The implications of and possible explanations for these interspecific differences in stomatal responses to soil water limitation are now discussed, together with the use of S_ψ to characterise them.

The significant reduction of stomatal conductance of both species by pre-dawn water potentials below -0.55 MPa indicated relatively strong stomatal control of transpiration in response to soil drought. When ψ_{max} decreased to -1.0 MPa total daily stomatal conductance of upper canopy foliage (g_{su}) was approximately 60 and 30% of the unlimited value for *E. globulus* and *E. nitens* respectively (eg. Figure 6.6). For the same value of ψ_{max}, Pereira et al. (1987) found that maximum daily g_s of *E. globulus* was reduced from 245 to 50 mmol m^{-2} s^{-1}, indicating a greater stomatal sensitivity to soil water limitation than in the current study. This may simply reflect a greater average vapour pressure deficit in the mediterranean (Portuguese) environment in the Pereira et al. (1987) study than in the current study.

Characterisation of the stomatal response of both species as relatively sensitive to soil drought is reinforced when reported responses of other *Eucalyptus* species are considered. Pook et al. (1966) reported a wide variation in stomatal responses of

Eucalyptus spp. to the 1965 drought in New South Wales. Subsequent studies in a range of communities have confirmed this observation. At one extreme several species exhibit strong stomatal control of transpiration, (*E. pauciflora* Sieb. ex. Spreng (Körner and Cochrane 1985), *E. obliqua* L'Herit. (Sinclair 1980) while *E. globulus* is prominent among a group of species characterised as having 'intermediate' stomatal control of transpiration during drought (Pereira et al. 1986, Pereira and Pallardy 1989, Pereira de Almeida and Riekerk 1990). Other species in this 'intermediate' group include *E. patens* Benth. and *E. rudis* Endl. (Carbon et al. 1981), and *E. maculata* Hook., *E. resinifera* Sm. and *E. saligna* Sm. (Colquhoun et al. 1984). At the other end of the spectrum are species in which stomatal control of transpiration is all but absent. This group includes *E. microcarpa* (Attiwill and Clayton-Greene 1984), *E. marginata* Don ex Sm. and *E. calophylla* R. Br. ex Lindl. (Colquhoun et al. 1984) and *E. leucoxylon* F. Muell. (Sinclair 1980). If *E. globulus* may be described as having 'intermediate' stomatal sensitivity to drought then *E. nitens* belongs in the group exhibiting strong control of transpiration. This study indicates that, like *E. pauciflora* (Körner and Cochrane 1985), *E. globulus* and *E. nitens* both adjust to drought via stomatal control of transpiration rather than through any significant change in the osmotic properties of their leaves (Chapter 3).

While stomatal conductance was quite sensitive to decreasing ψ_{max} in both species, as water stress increased a significant water stress by species interaction effect on g_s was evident due to a greater reduction of g_s in *E. nitens* than *E. globulus*. The diurnal pattern of this reduction also differed between the species. When ψ_{max} of the R treatment was significantly lower than in the I treatment the ratio of $g_{su,r}'$ to $g_{su,i}'$, which should reflect the effect of soil water on g_{su}, fluctuated during the day but was consistently lower in *E. nitens* than *E. globulus*. The observed fluctuation in this ratio is inconsistent with the observation that daily maximum g_s was correlated with ψ_{max} while daytime stomatal closure occurred below a threshold value of bulk leaf water potential, (ψ_l = -2.2 MPa) (Running 1980). This observation (in *Pinus contorta* Dougl.) was incorporated into FOREST BGC (Running and Coughlan 1988) and implies that stomata respond to a threshold bulk

leaf water potential and that this threshold value is reached at lower g_s as ψ_{max} decreases. In both species studied here g_s was significantly reduced on December 11, 1991, when ψ_{max} was -0.59 and -0.58 MPa (Table 6.1) and the minimum value of bulk leaf water potential was -1.58 and -1.86 MPa in *E. globulus* and *E. nitens* respectively (Chapter 3). At this time the osmotic potential at turgor loss point was approximately 2 MPa in both species (Figure 3.2). There was thus no evidence of the threshold response to bulk leaf water potential so often reported. The notion of an indirect response to soil moisture implicit in a threshold response to bulk leaf water potential has largely been replaced by the concept of a direct stomatal response to soil drying (Gollan et al. 1986) which is probably mediated by a chemical message originating in the roots. The chemical most often implicated is abscisic acid (ABA) (Raschke 1987, Jones and Davies 1991). The essential difference between this view and that of Running (1980) is that stomata are now understood to play an active role in regulating leaf water status rather than the converse. Moreover studies made under controlled conditions indicate that stomatal conductance may be unrelated to bulk leaf water potential (Gollan et al. 1985, Schulze et al. 1987). Monteith (1995b) has commented that stomata commence closure at a maximum transpiration rate and that the magnitude of this rate of transpiration is reduced by soil drying. Thus current understanding suggests that the reduced stomatal opening for both species below a pre-dawn leaf water potential of -0.55 MPa may be interpreted as a combination of a direct response to soil drying and an increased sensitivity to the rate of water loss from the wet surfaces surrounding sub-stomatal cavities. One or both of these mechanisms is apparently more sensitive in *E. nitens* than *E. globulus*.

When trees were rewatered after a period of water stress, stomatal conductance was much slower to recover in *E. nitens* than *E. globulus* (Table 6.1, Figure 6.4). This very important difference was evident as a pronounced hysteresis in the relationship between f(W) and ψ_{max} within any given stress cycle (Figure 6.6). To interpret the relatively slow recovery of *E. nitens* from water stress in the context of this observation it is instructive to reconsider the work of Whitehead et al. (1984). Stem flow rate predicted by Darcy's law was equated to transpiration and a

relationship derived to express the leaf area to sapwood area ratio (A_l/A_s) as a function of average vapour pressure deficit (D), stomatal conductance (g_s) and the gradient of xylem pressure potential ($\Delta\psi$) and sapwood permeability (k) over a given length (l) as follows:

$$\frac{A_l}{A_s} = \frac{k_h \Delta\Psi}{l} \cdot \frac{c}{D g_s} \qquad (6.7)$$

where c in turn was a function of several physical constants (see Chapter 4). The principal variables in this equation vary over different time periods making equation 6.7 difficult to interpret at any given time. Considering each of these variables integrated over a single stress cycle may provide some insights as to the relative effect of a period of increasing water stress on hydraulic conductivity (k_h) of *E. globulus* and *E. nitens*. Assuming that A_l/A_s and l are constant over this period:

$$k_h \propto \frac{D g_s}{\Delta\Psi} \qquad (6.8)$$

In the current study both treatments of both species were exposed to the same regime of ambient D throughout the experiment. The combination, under drought stress, of lower g_s and higher $\Delta\psi$ in *E. nitens* compared with *E. globulus* might therefore be anticipated to result in a markedly lower hydraulic conductivity in *E. nitens* at the point of re-watering. Reports of reduced hydraulic conductivity as a result of water stress are numerous (eg. Reich and Hinckley 1989, Tyree et al. 1991). Evidence is mounting that this reduction in hydraulic conductivity is at least partly due to embolism in the conducting xylem (Sperry and Tyree 1990). Tyree and Sperry (1988) found that plants operate very near the point of catastrophic or 'runaway' embolism and Sperry et al. (1993) argued that this point represents an unambiguous limit to the drought tolerance of plants. From the current study it seems that this point occurs at a lower water potential in *E. nitens* than *E. globulus*. The strategy of dessication avoidance adopted by *E. nitens* generates significantly greater values of $\Delta\psi$ than the strategy of drought tolerance adopted by *E. globulus*

(Chapter 3). This may result in a greater reduction in hydraulic conductivity in *E. nitens* due to cavitation and explain, at least in part, the slow recovery of this species after rewatering.

Instantaneous measures of soil water limitation, like ψ_{max}, for predicting stomatal responses to soil drying are commonly used in the ecophysiological literature (eg. Running 1980, Stewart 1988). Results from the current study showed that where several cycles of increasing soil moisture deficit followed by rainfall are experienced in any given growing season, ψ_{max} can be a poor predictor of g_s. A more effective means of explaining variation in g_s at a daily time step was achieved by using a cumulative measure of stress, S_ψ. Using S_ψ meant that the effect of water stress could be carried over into the recovery period, damping the increase in conductance for a period after rewatering and recovery of ψ_{max}. The correlation between f(W) and S_ψ was best when S_ψ was calculated over 8 and 20 days for *E. globulus* and *E. nitens* respectively.

In this study, it was important to quantify the effects of stress in such a way that the observed differences between species could be used to assess their suitability for planting on any given site. Given that S_ψ has been used with some success to quantify the effect of water stress on seedling (Perry et al. 1994) and tree growth (Unwin and Kriedemann 1990, Benson et al. 1992), and that stomatal conductance is an important physiological response limiting carbon assimilation under moderate water deficit in a range of tree species, including *E. globulus* (Pereira et al. 1987), it is surprising that S_ψ has not previously been used to quantify the effect of water stress. This study illustrates that S_ψ can be a valuable tool for accommodating observed hysteresis in the response of g_s to and recovery from water stress. As such S_ψ provides a simple empirical way of accounting for the residual effects of water stress, the mechanisms for which may be poorly understood. Weighting of individual days in calculation of S_ψ could be altered in many ways (eg. a negative exponential weighting). Presumably similar approaches might be applied to quantifying the residual effect of other environmental stresses (eg. high and low temperature) on a range of plant responses.

For both species the y-intercept of relationships between f(W) and S_ψ were greater than 1 (Figure 6.8). Increasing the base value for calculation of S_ψ (-0.2 MPa was used here) decreases the y-intercept. No adjustment in the base values was attempted here because, in *E. globulus* g_s of trees in the R treatment did reach higher values than in trees in the I treatment (Figure 6.4). Since trees in the R treatment were usually subjected to a further stress cycle, rather than remaining well watered for a sustained period, it is not possible from this data set to accurately describe the way g_s of *E. globulus* returns to pre-stress values after removal of water stress.

The effect of predicted reductions in g_{su} under soil water limitation on canopy transpiration and the relationship between canopy carbon assimilation and transpiration will depend on the size of the well watered canopy which is used as a basis for comparison, *viz.* a well watered canopy with the same L* as the water stressed canopy under consideration or a canopy which has never been water limited and so has a higher L* than the water stressed canopy. The latter comparison will be considered here as it is more relevant to the current study and includes the cumulative effect of previous stress cycles on L*. If canopy conductance calculated using a multilayered model (g_c, equation 5.2 or 6.6) is underestimated by equation 5.12 (g_c', see section 5.5), and by analogy equation 6.5 at L* greater than 6, then the predicted ratio of daily canopy conductance of rainfed trees to daily canopy conductance of irrigated trees will underestimate the effect of water stress (overestimate the ratio) on the same ratio calculated as the sum of the conductances of individual canopy layers (Figure 6.9). For example L* of the I and R treatment of *E. globulus* on January 1, 1993, was 6.4 and 4.9 respectively (Figure 4.3). At this time the relationship between predicted canopy conductance (g_c') and L* was on the linear phase in the R treatment while in the I treatment g_c' was approaching a maximum (Figure 5.9). As predicted g_c' (equations 5.12 and 6.5) gives greater weighting to the stomatal conductance of well lit upper canopy foliage (McNaughton 1994, Raupach 1995), the ratio of g_c' for R to the I treatment will reflect the effect on transpiration predicted by the Penman-Monteith

equation (equation 5.1, Monteith 1965) while the ratio of g_c for the R to the I treatment will more closely indicate the proportional effect on canopy photosynthesis. This suggests that at the canopy scale repeated cycles of water stress will reduce the water use efficiency.

Compared with *E. globulus*, *E. nitens* has faster closure and slower reopening of its stomata in response to water stress and after rewatering, respectively. The cumulative effect of these differences is quite dramatic. Relative to the I treatment of the same species, total predicted G_c' from October 1, 1992, to April 30, 1993, a period during which three stress cycles occurred, was reduced by 36 and 55% for *E. globulus* and *E. nitens* respectively. If, as has been reported for *E. globulus* (Pereira et al. 1987), limitation of carbon assimilation occurs principally in the gaseous phase then biomass production of *E. nitens* will be more limited by water stress than that for *E. globulus*. The implications of observed differences in stomatal responses between the species for relationships amongst canopy conductance, growth and water use warrant further consideration. Relationships amongst leaf area index, canopy conductance and transpiration will be considered in the next chapter (chapter 7). The implications for stem volume growth will depend on the effect of water stress on the relative patterns of carbon allocation in the two species. This will be considered in the concluding chapter (chapter 8).

Chapter 7. Regulation of transpiration by boundary layer and stomatal conductance in irrigated *E. globulus*: implications for calculation of transpiration in irrigated and water limited *E. globulus* and *E. nitens*

7.1 Introduction

In chapter 6 the effect of water stress on the stomatal conductance of upper canopy foliage was accommodated by adding a single function to a phenomenological model developed for irrigated trees (chapter 5). The model attenuated total daily stomatal conductance as a function of a cumulative water stress integral (Myers 1988). The form of this function was the same for the two species but the cumulative water stress integral was calculated over 8 days for *E. globulus* and 20 days for *E. nitens* (Table 6.2). The extent to which the stomatal response to water stress, observed and quantified in chapter 6, can be interpreted as a regulation of transpiration has to be considered at the canopy scale relative to the behaviour of irrigated trees growing under the same atmospheric conditions. To predict the extent to which stomatal closure at the leaf level can reduce transpiration we must understand the relationship between conductance and transpiration at the canopy scale in a stand which has never been water limited. The Penman-Monteith equation (Monteith 1965) remains the best and most widely applied model for estimating transpiration from physiological and meteorological data (Jarvis et al. 1981, Denmead 1984). Before applying the Penman-Monteith equation to a forest canopy there are two issues which deserve consideration.

The first, the principal assumption of the Penman-Monteith equation, is that sources and sinks of heat and water vapour are similarly distributed over the conducting surface to which the model is applied. If the canopy is treated as a single layer, in what has become known as a 'big leaf' model, then this assumption

is clearly violated (Jarvis et al. 1981). This problem has generally been overcome by applying the equation to individual canopy elements, usually layers, and summing the results to give an estimate of canopy transpiration (eg. Roberts et al. 1992). Raupach and Finnigan (1988) have discussed the relative merits of single versus multiple layer models and concluded that multiple layer models are appropriate where the forest canopy is the dominant element in the system. An alternative approach is to calculate an effective canopy conductance in 'big leaf' energy balance models: such an improved estimate should weight sunlit upper canopy foliage more heavily than foliage lower in the crown (McNaughton 1994). Three such schemes have been proposed (Raupach 1995), one of which was incorporated in the model of canopy conductance for irrigated trees developed in chapter 5 (equation 5.12).

The second issue concerns the relative importance of boundary layer and stomatal conductance in regulating transpiration. For tree crops, wind profile theory (Monteith and Unsworth 1990) predicts a turbulent airstream resulting in good mixing and the imposition of ambient atmospheric conditions at the canopy surface. Under such conditions a change in canopy conductance will result in an equiproportional change in transpiration (Jarvis 1985). In *Pseudotsuga menzeisii* (Tan and Black 1976, Tan et al. 1978) and *E. grandis* (Dye and Olbrich 1993) simple diffusive models driven by stomatal conductance and vapour pressure deficit were adequate to estimate transpiration. These results, together with the observation that transpiration is more sensitive to changes in stomatal than boundary layer conductance (eg. Dye 1987), have focused attention on estimation of stomatal and canopy stomatal conductance in the application of physiological techniques to forest hydrology. Where boundary layer conductance has been considered it has usually been estimated from wind profile theory (eg. Dye 1987).

That this view of transpiration by forest canopies is too simplistic is supported by the observation that annual evapotranspiration varied little among a range of deciduous hardwoods and conifers (Roberts 1983) and by the concept of a maximum surface conductance (Kelliher et al. 1995). The conservative nature of evapotranspiration was attributed to a negative feedback of transpiration on both

evaporative demand and surface conductance (Roberts 1983). Similarly, when available water was non-limiting, annual evapotranspiration of *E. nitens* was found to differ little from *E. delegatensis* R.T.Baker, despite an almost two fold difference in L* between the two species (Honeysett et al. 1992). These findings are consistent with the assertion that as the scale of observation is increased from the single leaf to the whole canopy the conducting surface may become increasingly decoupled from ambient conditions (Jarvis 1985). McNaughton and Jarvis (1983) proposed a dimensionless decoupling coefficient (Ω) to resolve transpiration estimated by the Penman-Monteith equation into its diffusion and radiation components.

Single layer models are computationally simpler than multiple layer models and more easily applied to assessing the impact of forest management decisions, including plantation establishment, on catchment or site water balance. In such models the issues presented above are inextricably linked. If perfect coupling can be assumed the canopy may be treated as a single layer without violating any assumption of the Penman-Monteith equation. The success of single layer models for estimating transpiration by forest canopies is a direct consequence of their aerodynamic roughness and strong coupling to ambient atmospheric conditions. If the scheme adopted in chapter 5 (equation 5.12) is applicable to *E. globulus* and *E. nitens* canopies, it follows that under conditions of perfect coupling predicted canopy conductance (g_c') should equate to that calculated as the sum of the conductances of individual canopy layers (g_c, equation 5.2). In chapter 5 it was observed that at L* > 5.5, g_c' underestimated g_c by as much as 41%, suggesting that at high L* *E. globulus* and *E. nitens* canopies become decoupled from ambient atmospheric conditions.

Decoupled canopies can be accommodated by the Penman-Monteith equation if either Ω or boundary layer conductance are known or may be predicted. Boundary layer conductance (g_a) has rarely been measured in eucalypt plantations (eg. Roberts and Rosier 1993) and no values for Ω have been reported for the genus. In this chapter, g_a and Ω are estimated for irrigated *E. globulus* in order to test two

commonly made assumptions in the application of the Penman-Monteith equation to forest canopies: that boundary layer conductance is very large in relation to stomatal conductance and that transpiration may be calculated from an simplified form of the Penman-Monteith equation which considers only stomatal conductance and vapour pressure deficit. These issues are considered for the whole canopy and for individual layers within the canopy.

7.2 Materials and Methods

7.2.1 Plant material

In March 1994 two experiments were undertaken in a group of three *E. globulus* trees selected from one of the three irrigated blocks (block 2, see Figure 2.2). A scaffold tower was erected around the three trees (trees one, two and three) to gain access to their crowns. In experiment one all three of the selected trees were measured. In experiment two all measurements were done on the first tree from experiment one.

7.2.2 Climate

For the duration of the experiments described in this chapter the weather station and net radiometer data loggers were reprogrammed (cf. chapter 2, section 2.2.5b) to sense all of wind speed (u), relative humidity (h), air temperature (T), vapour pressure deficit (D), total solar radiation (Q) and net radiation (R_n) every 5 minutes and record the average every 20 minutes commencing on the hour. The net radiometer was relocated to above the subject trees of the current experiment.

7.2.3 Leaf area

Leaf area of each of the three measurement trees was determined at the completion of the experiment. All the foliage was removed and separated into three layers corresponding to the upper, middle and lower third of the crown by depth. Specific leaf area (SLA) was calculated for a sub-sample of leaves from each layer on the basis of oven-dry weight at 80°C. The remaining leaves were dried to constant weight at 40°C. A subsample of this bulk leaf mass was weighed separately (W_{40})

and then dried at 80°C before reweighing (W_{80}). The ratio W_{80}/W_{40} was used to convert the bulk leaf weight to an oven-dry equivalent which was then multiplied by SLA to give leaf area. Total leaf area of each tree was calculated as the sum of leaf area from the three canopy layers.

The linear relationship between leaf area and sapwood area developed in July 1993 excluding litter (Table 4.3) was applied to growth data collected on March 29, 1994, to calculate mean L* for I *E. globulus* at this time. This was apportioned to each of the canopy layers using coefficients also derived in July 1993 (Table 4.4).

7.2.4 Conventions

For experiment one, conductance and transpiration are expressed on a ground area basis and the subscript i refers to the i^{th} tree where I=1, 2 or 3. For experiment two conductance and transpiration are expressed per unit leaf area. For both experiments the subscript j refers to the j^{th} canopy layer where j=1, 2and 3 for the upper, middle and lower third of the canopy by depth.

7.2.5 Experiment one. Regulation of transpiration at the canopy scale

On March 1, 4 and 9, 1994, sap flow and stomatal conductance were measured concurrently. From this data canopy transpiration, stomatal and boundary layer conductance were calculated as follows.

Sap flow of each tree was estimated using a standard (SF100) Greenspan Sapflow sensor (Greenspan Technology, Warwick, Queensland, Australia). Two probesets were installed in each tree. Each probeset comprised a line heater and two parallel stainless steel tubes. One half each of two thermistor pairs was housed in each tube, one of which was 10 mm downstream of the line heater while the other was 5 mm upstream of the heater. Within each tube the thermistors pairs were separated by 5 mm. The probesets were installed on opposite aspects (East and West if possible) so that the thermistor pairs were 10, 15, 20 and 25 mm under the cambium.

At 20 minute intervals a heat pulse of 0.8 seconds duration was generated. Sap flow (S) was calculated after Marshall (1958), Swanson and Whitfield (1981) and Swanson (1983) as described by Olbrich (1991).

Canopy tranpiration (E) was expressed on a ground area basis as follows:

$$E = L^* \left(\frac{\sum_{i=1}^{3} S_i / L_i}{3} \right) \qquad (7.1)$$

where S_i was sap flow measured for the i^{th} tree and L_i total leaf area of that tree. L* was stand leaf area index at the time of the experiment (≈8.0). Hourly transpiration was calculated as the average of four instantaneous measurements from the commencement of the hour. Transpiration estimated from sap flow measurements is subsequently called observed transpiration. In *E. grandis* estimates of transpiration made from heat pulse velocity measurements corresponded very closely with actual water use determined gravimetrically (Olbrich 1991). *E. globulus* might be expected to behave similarly in this respect to *E. grandis* since both species are diffuse porous hardwoods. Cut tree experiments in *E. globulus* suggest that transpiration estimated from sap flow closely approximates gravimetric water use (Zang Daoqun, personal communication).

Stomatal conductance (g_s) was measured on six leaves from each tree (18 leaves in all). One leaf was selected from each of two aspects (East and West) within each of three canopy layers corresponding to the upper, middle and lower third of the crown by depth. Stomatal conductance per unit leaf area (g_s) was calculated as the sum of stomatal conductance for the adaxial and abaxial surfaces. Measurement of tree one commenced on the hour, tree two 20 minutes and tree three 40 minutes after the hour. Mean hourly stomatal conductance was calculated for each canopy layer as the average of the six leaves measured within that layer.

Average hourly canopy stomatal conductance was then calculated using the two approaches considered in chapter 5. In the first instance canopy stomatal conductance (g_c) was calculated as the sum of the parallel conductances of j individual canopy layers (equation 7.2), where $g_{s,j}$ and L^*_j were the mean stomatal conductance and leaf area index of the j^{th} canopy layer. The second approach was to multiply the mean stomatal conductance of the upper canopy (g_{su}) by f(Q) integrated over the canopy with respect to the cumulative leaf area index (ξ). f(Q) was the light response function described and discussed in chapter 5 (equation 5.3). Subsequently canopy stomatal conductance calculated with equation 7.3 will be distinguished from that calculated with equation 7.2 by a 'prime' symbol (g_c, equation 7.2 cf. g_c', equation 7.3). The same convention will be applied to all quantities derived from these estimates of canopy stomatal conductances.

$$g_c = \sum_{j=1}^{3} g_{s,j} L^*_j \tag{7.2}$$

$$g_c' = g_{su} \int_0^{L^*} f(Q_\xi) d\xi \tag{7.3}$$

Canopy surface conductance (g_{sc}), inclusive of boundary layer and stomatal conductance, was calculated after Meinzer et al. (1993) where P is atmospheric pressure.

$$g_{sc} = \frac{E}{D/P} \tag{7.4}$$

Assuming boundary layer and stomatal resistance to be in series, boundary layer conductance of the canopy (g_a) was calculated.

$$g_a = \frac{1}{\frac{1}{g_{sc}} - \frac{1}{g_c}} \tag{7.5}$$

Ω, a dimensionless decoupling coefficient proposed by McNaughton and Jarvis (1983), was calculated assuming the canopy to behave as a single amphistomatous leaf symmetrical with respect to boundary layer conductance. The formula from Jarvis and McNaughton (1986), equation 7.6, was used as this gave the same answers, to the third decimal place, as the more complex formulation discussed by Martin (1989) and McNaughton and Jarvis (1991).

$$\Omega = \frac{\beta + 1}{\beta + 1 + g_a/g_c} \tag{7.6}$$

$$\text{where} \quad \beta = \Delta\lambda/(c_p P) \tag{7.7}$$

and Δ was the slope of the relation between saturated vapour pressure and temperature, λ the latent heat of vaporisation of water and c_p the specific heat of dry air.

Transpiration (E) was calculated in four ways. The first two, E_m (Meinzer et al. 1993) and E_{imp} (Jarvis and McNaughton 1986) assumed D was imposed at the canopy surface (ie. Ω=0). E_{imp} is equivalent to the form of the Penman-Monteith equation applied by Tan et al. (1978) which required the specific heat of moist air, c_{pa}, and the psychrometric constant (γ). Transpiration of *E. grandis* was calculated as E_m by Dye and Olbrich (1993).

$$E_m = g_c \left(D/P\right) \tag{7.8}$$

$$E_{imp} = \frac{\left(c_{pa}/\gamma\right) g_c D}{\lambda} \tag{7.9}$$

The equilibrium transpiration rate for completely decoupled canopies was then calculated (equation 7.10) and combined with E_{imp} in equation 7.11 to give E_Ω, an estimate of transpiration which partitions transpiration between the radiation and deficit components of the Penman-Monteith equation using the dimensionless decoupling coefficient, Ω (McNaughton and Jarvis 1983, Jarvis and McNaughton 1986).

$$E_{eq} = \frac{\varepsilon R_n}{(\varepsilon + 1)\lambda} \tag{7.10}$$

$$E_\Omega = \Omega E_{eq} + (1 - \Omega) E_{imp} \tag{7.11}$$

For comparison with D measured at the weather station, vapour pressure deficit imposed at the canopy surface (D_s) was calculated as:

$$D_s = \frac{EP}{g_c} \tag{7.12}$$

7.2.6 Experiment two. Vertical profile of regulation of transpiration

Vertical profiles of g_s, g_a and Ω were examined for tree one throughout March 17, 21 and 24, 1994.

The sapflow sensors were installed at two thirds of tree height, one third of tree height and just above ground height. Sensors were installed using the same protocol as experiment one and transpiration by each canopy layer was calculated as follows:

$$E_j = \left(S_j - S_{j+1}\right) / L_j \tag{7.13}$$

where S_j was sapflow measured at the bottom of the j^{th} canopy layer and L_j leaf area determined for the j^{th} layer.

Stomatal conductance was measured on four leaves, one from each of the four cardinal directions, in each canopy layer. Stomatal conductance ($g_{s,j}$) per unit leaf area was determined for each of the j layers as the average of g_s measured for each of these four leaves.

Surface conductance ($g_{sc,j}$) and boundary layer conductance ($g_{a,j}$) and the decoupling coefficient (Ω_j) were calculated for the j^{th} canopy layer over the course of the three measurement days using equations 7.4, 7.5 and 7.6. Similarly $E_{m,j}$, $E_{imp,j}$, $E_{eq,j}$ $E_{\Omega,j}$ and $D_{s,j}$ were calculated for each layer using equations 7.8, 7.9, 7.10, 7.11 and 7.12 respectively. For calculation of $E_{eq,j}$ and $E_{\Omega,j}$, net radiation absorbed by the j^{th} layer ($R_{n,j}$) was calculated from the Beer-Lambert law (Landsberg, 1986) using an extinction coefficient of 0.5.

7.2.7 Statistical analysis

Relationships between E, g_a, g_c, Ω, E′, g_a', g_c', Ω' and a range of environmental variables measured at the weather station were explored by linear and multiple linear regression. Variables derived from g_c were compared to those derived from g_c' (eg. E cf E′) using a t-test for paired data. In experiment two the effect of layer on Ω, E, E_{imp}, E_{eq}, R_n, and g_a was also investigated using t-tests for paired data.

7.3 Results

7.3.1 Experiment 1. Regulation in the canopy

7.3.1a Environment.

Between 9 am and 4 pm on March 1, 4 and 9, 1994, the environment was quite mild. Air temperature varied between 13.4 and 21.7°C while D was less than 1.2 kPa and Q between 935 and 2006 μmol m^{-2} s^{-1} (Table 7.1). Soil water deficit was 11 mm on February 17, 1994, and 10 mm on March 11, 1994.

Table 7.1. Minimum, mean and maximum values of air temperature (T), wind speed (u), relative humidity (h), vapour pressure deficit (D), total solar radiation (Q) and net radiation (R_n) recorded during the measurement periods on March 1, 4 and 9, 1994.

Variate	Minimum	Mean	Maximum
T (°C)	13.4	17.3	21.7
u (m s^{-1})	1.4	3.4	5.1
h (%)	47	57	77
D (kPa)	0.48	0.85	1.18
Q (μmol m^{-2} s^{-1})	935	1413	2006
R_n (Wm^{-2})	285	456	645

7.3.1b Diurnal patterns.

Canopy stomatal conductance (g_c) varied very little between 8am and 4pm on the three measurement days. On March 1, 4 and 9, 1994, respectively maximum g_c was 1750, 1898 and 1466 mmol m^{-2} s^{-1} while for the same days mean g_c was 1601 ± 52, 1744 ± 82 and 1366 ± 121 mmol m^{-2} s^{-1} (Figures 1a, c and e).

Boundary layer conductance (g_a) varied more markedly than g_c (Figure 7.1). On March 4 and 9, g_a increased throughout the measurement period reaching 3706 mmol m^{-2} s^{-1} on both days. On March 9 this steady increase occurred in spite of fluctuations in Q (Figures 1e and f). On both March 4 and 9 D and u increased

throughout the day (Figures 1 d and f). On March 1 peak u was 5.1 m s^{-1} at 11 am and declined steadily thereafter to be 3.0 m s^{-1} at 1500 h while D increased as on the other days. Thus g_a appeared to respond more to variation in u compared to D and Q (Figure 7.1).

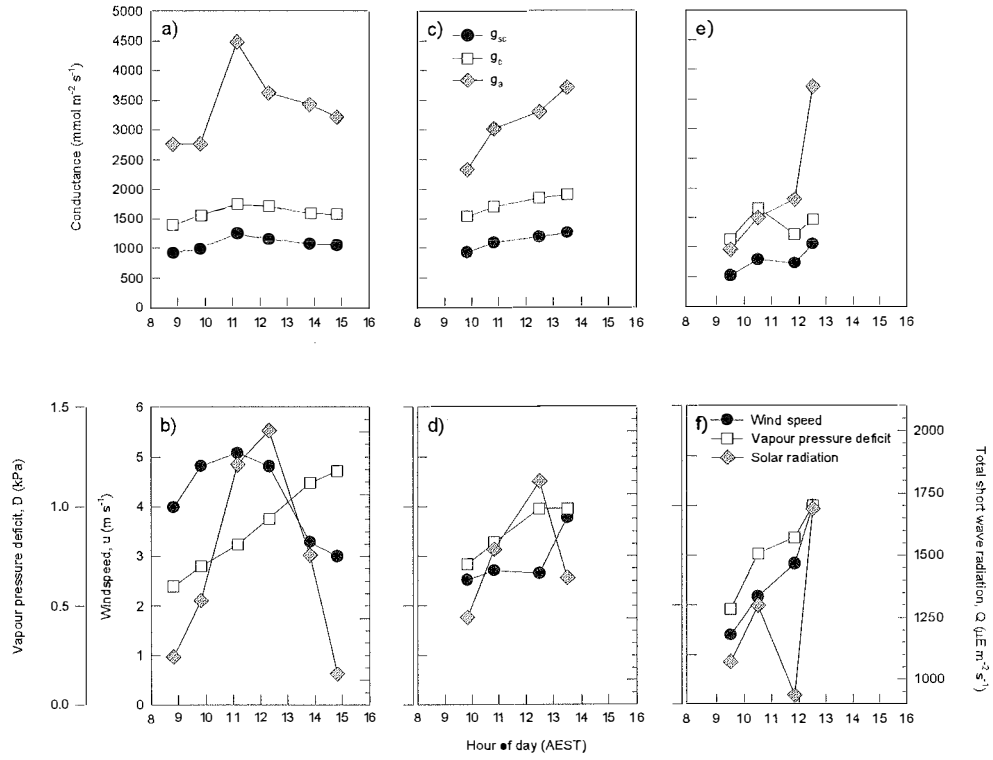

Figure 7.1. Diurnal course of canopy surface conductance (g_{sc}), canopy stomatal conductance (g_c) and boundary layer conductance (g_a) on a) March 1, c) March 4 and e) March 9. b), d) and f) Diurnal course of total solar radiation (Q), vapour pressure deficit (D) and wind speed (u) for the same days.

The ratio of canopy boundary layer to canopy stomatal conductance (g_a/g_c) showed similar diurnal trends to g_a and peaked at 11 am on March 1 and increased throughout the other measurement days (Figure 7.2a). Fluctuations in g_a/g_c were not as marked as those for g_a. Minimum and maximum g_a/g_c observed were 0.9 and 2.6 respectively. Diurnal fluctuations in Ω were opposite to those observed for g_a/g_c. The minimum and maximum values of Ω observed were 0.59 and 0.78

respectively while the mean value over the three days was 0.63 ± 0.02 (Figure 7.2b).

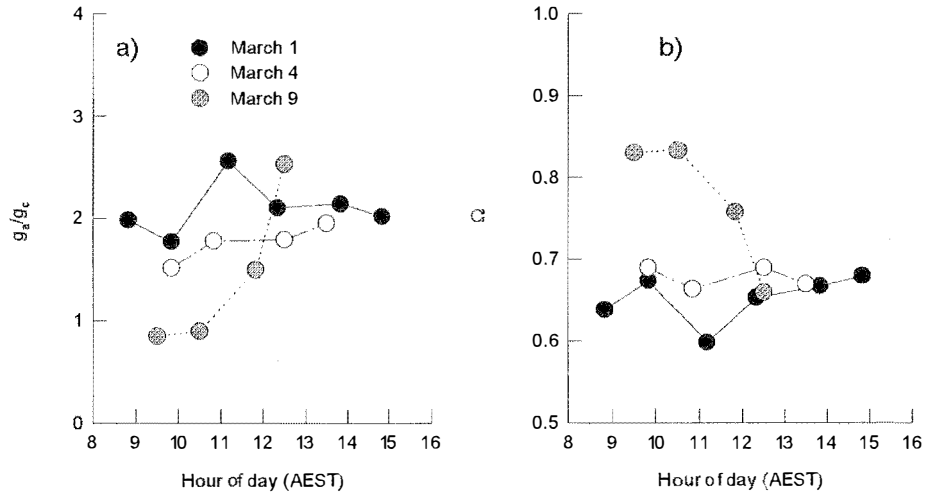

Figure 7.2. Diurnal course of a) the ratio of canopy boundary layer to canopy stomatal conductance (g_a/g_c) and b) the dimensionless decoupling coefficient or omega factor (Ω) for March 1, 4 and 9, 1994.

The diurnal patterns of variation in g_c', g_a', (g_a'/g_c') and Ω' were similar to those described above for g_c, g_a, g_a/g_c and Ω. Mean canopy conductance calculated with equation 7.3 (g_c') was significantly lower than g_c. Consequently boundary layer conductance derived from g_c' (g_a') and (g_a'/g_c') were significantly greater than g_a and g_a/g_c respectively while Ω' was significantly lower that Ω (Table 7.2).

Table 7.2. A comparison of mean values (± standard error) of canopy stomatal conductance (g_c, g_c'), boundary layer conductance (g_a, g_a'), the ratio of boundary layer conductance to canopy stomatal conductance (g_a/g_c, g_a'/g_c') and the dimensionless decoupling coefficient (Ω, Ω') derived from canopy conductances calculated with equations 7.2 (the sum of parallel resistances) and 7.3 (after Raupach (1995).

Variable	Equation 7.2		Equation 7.3′	
Canopy stomatal conductance (mmol m^{-2} s^{-1})	g_c	1575 ± 59	g_c'	1093 ± 57
Boundary layer conductance (mmol m^{-2} s^{-1})	g_a	2897 ± 258	g_a'	10600 ± 2763
g_a/g_c	g_a/g_c	1.8 ± 0.2	g_a'/g_c'	9.8 ± 1.7
Dimensionless decoupling coefficient (Ω)	Ω	0.63 ± 0.02	Ω'	0.26 ± 0.06

7.3.1c Regulation of transpiration.

Boundary layer conductance, g_a/g_c and Ω were better correlated with u and h than any other weather variables. Correlation coefficients between g_a, g_a/g_c, Ω and u were, respectively, 0.756, 0.783 and -0.803 while correlation coefficients between the same three variables and h were -0.749, -0.613 and 0.655. Linear relationships with wind speed explained 57, 61 and 62% of the observed variation in g_a, g_a/g_c and Ω (Table 7.3). Of the remaining independent variables only addition of h contributed significantly to the explanation of variation in g_a, g_a/g_c or Ω. Inclusion of h improved r^2 values for g_a, g_a/g_c and Ω to 0.80, 0.69 and 0.76 respectively (Table 7.3). Inclusion of an interaction term (h*u) did not significantly improve the fit for any of g_a, g_a/g_c or Ω.

Table 7.3. Constants, coefficients and r^2 values for relationships to predict boundary layer conductance (g_a) (mmol m^{-2} s^{-1}), g_a/g_c (dimensionless) and the dimensionless decoupling coefficient (Ω) from windspeed (u, m s^{-1}) only and from u and relative humidity (h, %).

Dependent variable	Constant	Coefficient for u	Coefficient for h	r^2
g_a	645	670	NF	0.57
g_a	4566	497	-58.9	0.80
g_a/g_c	0.59	0.36	NF	0.61
g_a/g_c	2.021	0.30	-0.02	0.69
Ω	0.81	-0.052	NF	0.62
Ω	0.59	-0.042	0.003	0.76

NF - not fitted

7.3.1d Canopy transpiration.

Canopy transpiration (E) increased throughout the measurement period on all three days. Maximum recorded values on March 1, 4 and 9 were 12.4, 12.3 and 10.4 mmol m^{-2} s^{-1} respectively.

Canopy transpiration calculated assuming imposition of D at the canopy surface (E_m and E_{imp}) significantly overestimated E. Mean E_m, E_{imp} and E over the three days were, respectively, 13.5± 1.1, 12.5± 0.9 and 8.7± 0.8 mmol m^{-2} s^{-1}. The difference between E_{imp} and E was relatively constant across the range of E, the slope of a linear relationship expressing E_{imp} as a function of E being 1.03 (Figure 7.3a). The slope of the relationship between E_m and E was 1.27 (Figure 7.3a) so that as E increased so too did the gap between D and vapour pressure deficit actually imposed at the leaf surface (D_s). Mean D_s was 0.54± 0.05 kPa over the three days, significantly lower than mean D (0.85± 0.04 kPa). When the same assumption of perfect coupling was made and g_c' substituted for g_c, E_m' and E_{imp}' closely approximated E over its entire range (Figure 7.3b). Mean E_m' and E_{imp}' over the three days were, respectively, 9.2 ± 0.7 and 8.6 ± 0.6 mmol m^{-2} s^{-1}. Neither E_m' nor E_{imp}' were significantly different from measured transpiration (E, 8.7 ± 0.8 mmol m^{-2} s^{-1}).

While E_Ω and E were strongly correlated, the correlation coefficient between the two variables being 0.87, E_Ω overestimated E below 9.3 mmol m^{-2} s^{-1} and underestimated E at larger values (Figure 7.3a). Though E_Ω' also underestimated E above 9.3 mmol m^{-2} s^{-1} this effect was not as marked as with E_Ω (Figure 7.3b). E was significantly related to D (r^2=0.85) but not to R_n (r^2=0.14) (Table 7.4, Figure 7.4).

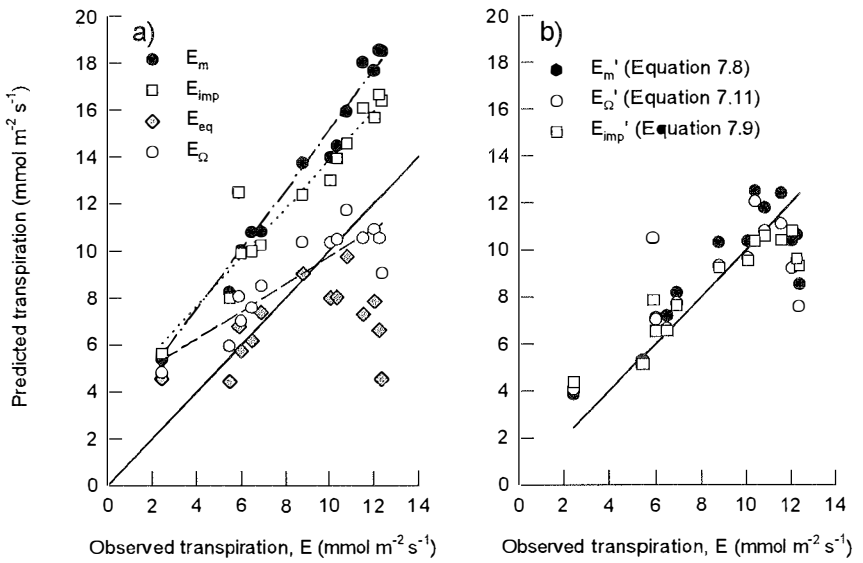

Figure 7.3. Predicted transpiration expressed as a) E_m, E_{imp}, E_{eq} and E_Ω and b) E_m', E_Ω', and E_{imp}' as a function of measured transpiration (E). Solid line is 1:1.

Table 7.4. Coefficients and r^2 values for relationships to predict transpiration (E) as a function of net radiation (R_n, Wm^{-2}), vapour pressure deficit measured at the weather station (D, kPa) and vapour pressure deficit calculated at the leaf surface (D_s, kPa).

Dependent variable	Independent variable	y-intercept	x-coefficient	r^2
E	D	-3.8	14.7	0.85
E	D_s	-1.19	18.0	0.90
E	R_n	3.86	0.01	0.14

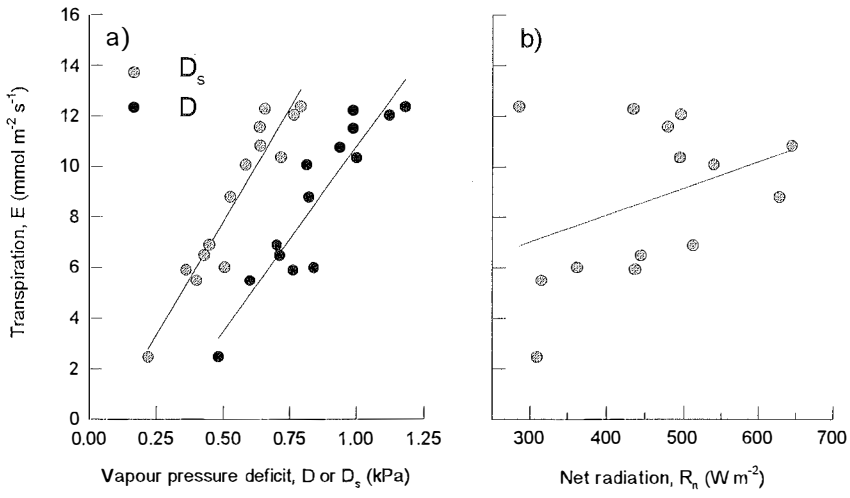

Figure 7.4. a) Transpiration (E) as a function of vapour pressure deficit at the canopy surface (D_s) and at the weather station (D). b) E as a function of net radiation (R_n).

7.3.2 Experiment 2. Variation in control between canopy layers

7.3.2a Environment.

For the three measurement periods on March 17, 21 and 24 conditions were mild (Table 7.5), although maximum u (6.5 ms^{-1}) and D (1.6 kPa) were slightly greater than during experiment 1. Q was always greater than 570 μmol m^{-2} s^{-1}. Average T was the same as for experiment 1 (17.3°C). R_n and D_s differed significantly between all canopy layers and decreased sharply from the upper to the lower canopy layer (Table 7.6).

Table 7.5. Minimum, mean and maximum values of air temperature (T), windspeed (u), relative humidity (h), vapour pressure deficit (D) and total solar radiation (Q) during Experiment 2 (March 17, 21 and 24, 1994).

Variate	Minimum	Mean	Maximum
T (°C)	7.7	17.3	23.0
u (ms^{-1})	1.0	3.3	6.5
h (%)	40	61	94
D (kPa)	0.10	0.85	1.60
Q (μmol m^{-2} s^{-1})	576	1291	1728

7.3.2b Effects of canopy layer.

Under these conditions 35, 59 and 6 % of total sapflow was attributed to the upper, middle and lower layers respectively. When considered per unit leaf area the mean rate of transpiration was significantly different between all canopy layers, and was 1.37, 0.89 and 0.11 mmol m^{-2} s^{-1} from the three layers respectively (Table 7.6).

Boundary layer and stomatal conductance were significantly affected by canopy layer and decreased significantly from the top through the middle and lower canopy. Ω increased significantly with canopy depth (Table 7.6).

Neither Ω nor g_a in the upper or lower layer was significantly related to u or h while in the middle layer a significant proportion of variation in both g_a (r^2=0.58) and Ω (r^2=0.63) was explained by linear relationships with u.

Table 7.6. Mean values of net radiation (R_n), vapour pressure deficit at the leaf surface (D_s), transpiration (E), boundary layer conductance (g_a), stomatal conductance (g_s) and the dimensionless decoupling coefficient (Ω) between 0900 h and 1600 h on March 17, 21 and 24 (± s.e.), by canopy layer.

Variate	Upper layer	Middle layer	Lower layer
R_n (Wm^{-2})	260 ±18	133 ±18	10 ±1
D_s (kPa)	0.75 ±0.07	0.57 ±0.06	0.14 ±0.04
E (mmol m^{-2} s^{-1})	1.37 ±0.60	0.89 ±0.05	0.11 ±0.02
g_a (mmol m^{-2} s^{-1})	771 ±154	525 ±162	25 ±10
g_s (mmol m^{-2} s^{-1})	201 ±11	146 ±15	81 ± 9
Ω (dimensionless)	0.29 ±0.03	0.40 ±0.05	0.84 ±0.05

7.3.2c Predicting transpiration.

Mean ratios of both E_m and E_{imp} to E increased significantly from the upper to the lower layer (Figure 7.5a,b) and were 1.34 and 1.24, 1.61 and 1.51 and 12.3 and 12.3 for the upper, middle and lower layers respectively. For all canopy layers E_Ω was a better predictor of E than either E_m or E_{imp} (Figure 7.5).

Coefficients of determination for linear relationships between E and D decreased with depth in the canopy and were 0.59, 0.47 and 0.06 respectively for the upper, middle and lower layer of the canopy (Figure 7.6a, Table 7.7). Conversely R_n was a better predictor of E for the bottom layer (r^2=0.49) than for either the middle (r^2=0.06) or upper canopy layer (r^2=0.28) (Figure 7.6, Table 7.7).

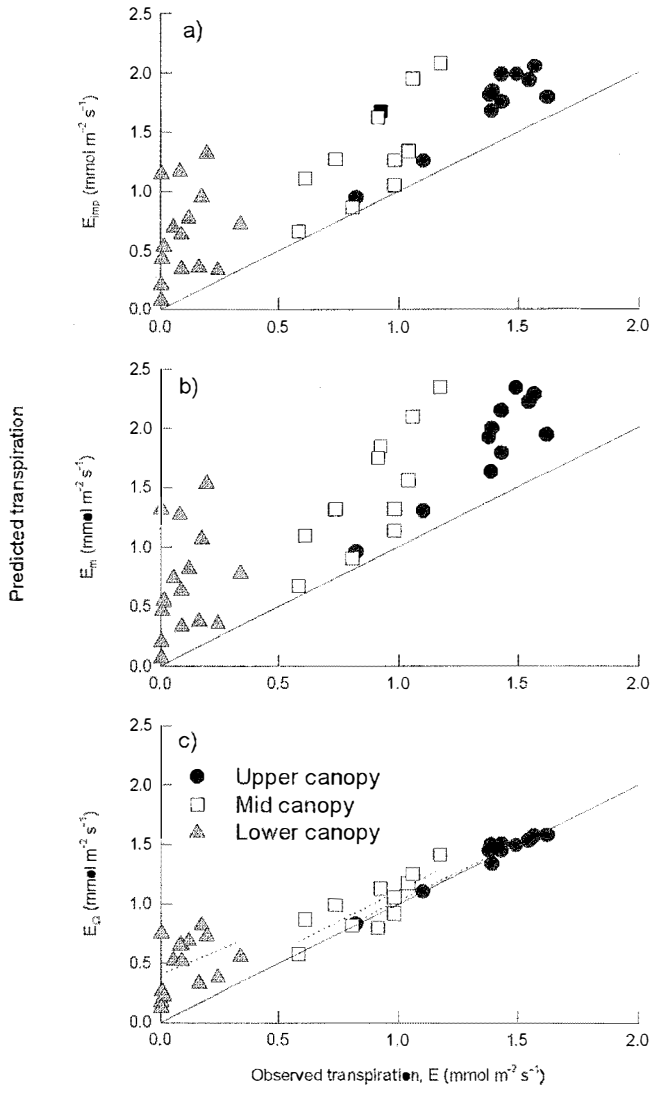

Figure 7.5 Predicted transpiration expressed as a) E_{inp}, b) E_m and c) E_Ω as a function of E for the upper, middle and lower canopy layer. Solid lines are 1:1 in each case.

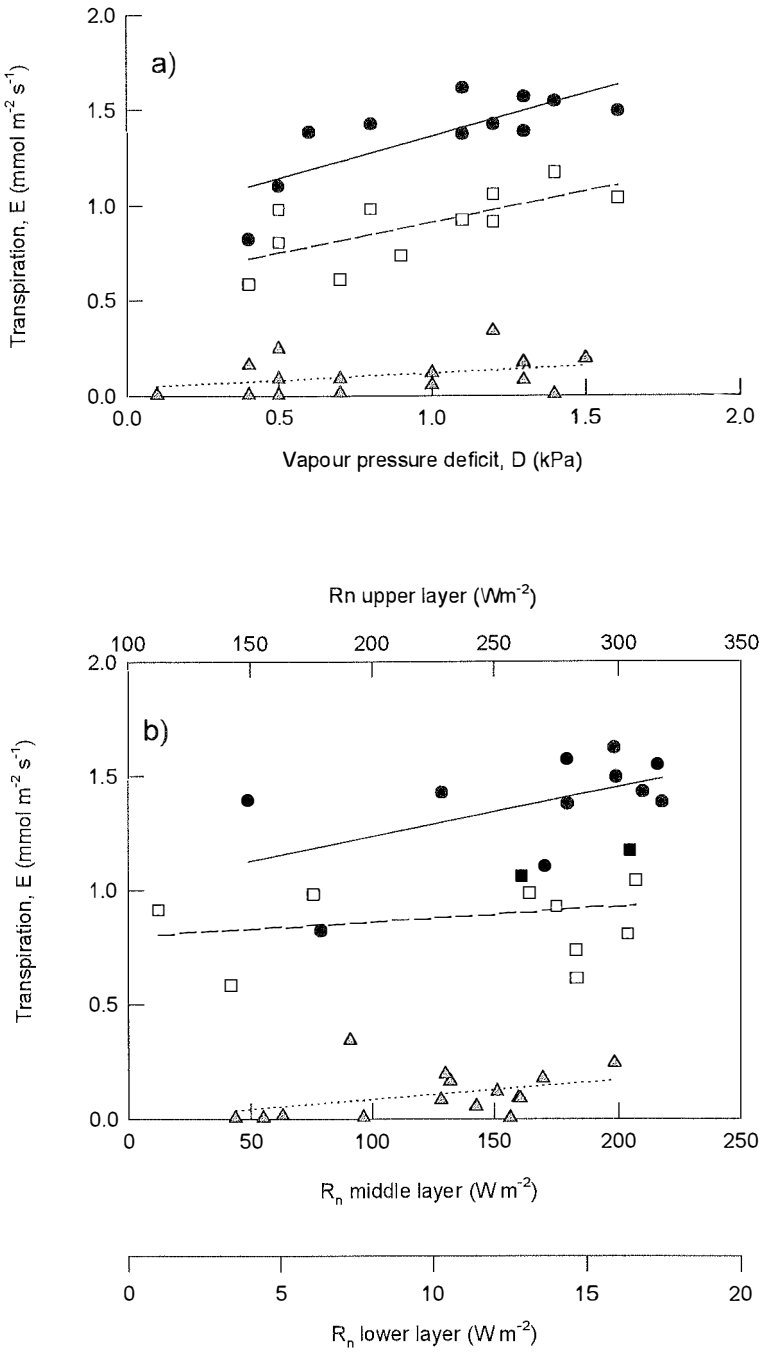

Figure 7.6 Transpiration (E) as a function of a) D and b) R_n for the upper, middle and lower canopy layers. Symbols as for Figure 7.6

Table 7.7. Coefficients and r^2 values for relationships expressing transpiration (E) as a function of vapour pressure deficit (D) and net radiation (R_{nj}), by canopy layer

Dependent variable	Independent variable	Layer	y-intercept	x-coefficient	r^2
E	D	Upper	0.92	0.44	0.59
		Middle	0.59	0.32	0.47
		Lower	0.053	0.04	0.06
E	R_n	Upper	0.8	2.14×10^{-3}	0.28
		Middle	0.79	6.62×10^{-4}	0.06
		Lower	-0.06	0.014	0.49

7.4 Discussion

The assumption of perfect coupling, which is the basis for successful application of the Penman-Monteith equation to forest canopies in single layer models, was not valid in this high L* *E. globulus* plantation. The mean value of Ω over March 1, 4 and 9, 1994, was 0.63 and consequently transpiration calculated assuming perfect coupling significantly overestimated values derived from sapflow measurements. Apportioning transpiration to the equilibrium and imposed rates using calculated values of Ω underestimated E at rates greater than 9.3 mmol m^{-2} s^{-1}. Thus even if Ω could be estimated for the whole canopy, errors would be made in the prediction of transpiration. The observed vertical profile of Ω and absorbed net radiation showed that this underestimation at high E was due to violation of the principal assumption of the Penman-Monteith equation, that sources and sinks of heat and water vapour are similarly distributed over the surface to which the model is applied. Reasonable estimates of observed transpiration were obtained either by applying the Penman-Monteith equation separately to the three layers or by artificially weighting the calculation of canopy conductance (g_c') towards well lit upper canopy foliage using the Beer-Lambert law. The latter approach is simpler but obscures details of variation in stomatal conductance, boundary layer conductance and Ω throughout the canopy and precludes the use of g_c' in combined models of canopy transpiration and assimilation. These issues are now discussed in more detail. In particular the implications for the relative effect of water stress on canopy transpiration and assimilation are considered.

For the canopy the minimum, mean and maximum values of Ω were 0.59, 0.63 and 0.78 respectively. Reported values of Ω are few though Ω may be calculated where g_s (or g_c) and g_a are known. From reported values of g_s and g_a for *E. camaldulensis* and *E tereticornis* (Roberts and Rosier 1993) in southern India, Ω may be deduced to have varied between 0.2 and 0.4. For *E. grandis* in South Africa Ω varied from approximately 0.1 to 0.35[1] (Dye and Olbrich 1993). For *Eucalyptus* plantations Ω was generally higher than for coniferous forests or plantations (eg. Ω was less than 0.1 for *Pinus* spp and *Picea sitchensis* (Meinzer 1993). In the irrigated *E. globulus* studied here mean Ω was comparable to that for the tropical species *Tectona grandis* L. (0.9), *Triplochiton scleroxylon* (0.6), *Gmelina arborea* Roxb. (0.9) and *Anarcadium excelsium* (Bertero and Balb.) Skeels (0.6) (Meinzer 1993, Meinzer et al. 1993).

Omega is a function of the reciprocal of the ratio of boundary layer to stomatal conductance. The shape of the relationship between Ω and g_s (or g_c) is largely determined by the value of g_a. At high values of g_a, Ω is a weak, approximately linear, function of g_c (or g_s). As g_a decreases the relationship between Ω an g_s approximates a rectangular hyperbola so that Ω is only affected by g_c (or g_s) when g_c (or g_s) is less than 500 mmol m^{-2} s^{-1} (Figure 7.7). In the current study mean g_c was 1573 mmol m^{-2} s^{-1} and varied little within or between measurement days (Figure 7.1). This is greater than the maximum values observed in southern India for *E. camaldulensis* (545 mmol m^{-2} s^{-1} in May 1988) and *E. tereticornis* (300 mmol m^{-2} s^{-1} in May 1988; Roberts and Rosier 1993) or in South Africa for *E. grandis* (1200 mmol m^{-2} s^{-1}; Dye and Olbrich 1993). For conifer needles g_s ranged from approximately 14 mmol m^{-2} s^{-1} for *Thuja occidentalis* L. and *Picea engelmannii* Engelm. to 333 mmol m^{-2} s^{-1} in *Pseudotsuga menzeisii* on a needle area basis (Jarvis et al. 1976)[2]. In *Pinus sylvestris* maximum g_c was approximately 300 mmol m^{-2} s^{-1} when D was less than 1 kPa (Beadle et al. 1985b). Thus the range

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[1]Stomatal conductance was reported on a leaf area basis for a single tree (Dye and Olbrich 1993). For calculation of Ω it was assumed that each of the 725 stems ha^{-1} occupied equal ground area and that g_a was 10 mol m^{-2} s^{-1} (no data was presented).

[2]Where conductance was reported in cm s^{-1} or m s^{-1} conversion to mmol m^{-2} s^{-1} was made assuming P=101.3 kPa and T=25°C.

of g_c reported for eucalypts is higher than for most coniferous stands . The values of g_s and g_c of the irrigated *E. globulus* in this study and *E. grandis* in South Africa were comparable to those found for rainforest species (Whitehead et al. 1981, Roberts et al. 1990). Inspection of these data suggest that these differences are largely a function of L*. L* was 8.0 in the irrigated *E. globulus* studied here, one of the highest values recorded for eucalypts (chapter 4).

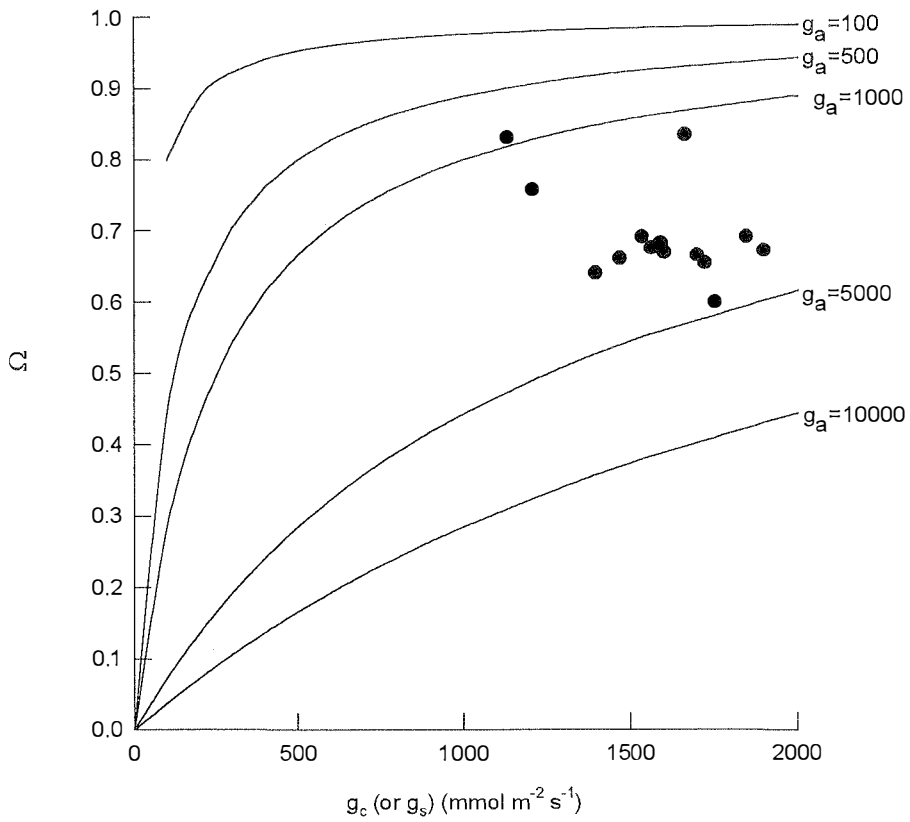

Figure 7.7 Omega as a function of canopy or stomatal conductance (g_c or g_s) for a range of boundary layer conductances (g_a, mmol m^{-2} s^{-1}). Solid circles are the hourly data from experiment 1.

Maximum g_a, the other determinant of Ω, recorded during experiment 1 was 4479 mmol m^{-2} s^{-1}, or 535 mmol m^{-2} s^{-1} on a leaf area basis. Also on a leaf area basis maximum g_a for *E. camaldulensis* was approximately 3900 mmol m^{-2} s^{-1} or between

3120 (L*=0.83) and 9160 mmol m^{-2} s^{-1} (L*=2.35) on a ground area basis (Roberts and Rosier 1993). The range of windspeed over which g_a was observed (0-5 m s^{-1}) was similar to this study. On a leaf area basis g_a for an Amazonian rainforest varied from 240 mmol m^{-2} s^{-1} at the forest floor to 1400 mmol m^{-2} s^{-1} at the top of the canopy (Roberts et al. 1990). In this study high g_c and low g_a acted together to give values of Ω comparable to those reported for a range of rainforest species (Meinzer 1993) (Figure 7.7).

The low values of g_a recorded for *E. globulus* may be a result of the depth (12 m) and density of the canopy (L*=8.0) restricting penetration of turbulent eddies into the canopy. The adult foliage of *E. globulus* is long, falcate and hangs vertically (Costermans 1981). Individual elements within the canopy would therefore have large drag coefficients (Thom 1971, Thom 1975) which coupled with high aerodynamic roughness (Thom 1975) might be expected to result in a turbulent airstream and a large downward flux of momentum.

When it was assumed that boundary layer conductance was very large in relation to stomatal conductance (ie. transpiration was calculated as E_m or E_{imp}), E was significantly overestimated (Figure 7.3a). This contrasts with results for *P. menzeisii* (Tan and Black 1976, Tan et al. 1978) and *E. grandis* (Dye and Olbrich 1993) where E was successfully estimated from the diffusive component of the Penman-Monteith equation (Monteith 1965), assuming ambient D to be imposed at the leaf surface throughout the canopy. When the same assumption was made in the current study transpiration was overestimated by between 3 and 6 mmol m^{-2} s^{-1} (Figure 7.3a).

E_Ω was a better predictor of E than either E_m or E_{imp}, but overestimated E below 9.3 mmol m^{-2} s^{-1} and underestimated E above this value. At the canopy scale only 14% of variation in E could be explained by a linear relationship with R_n while a similar relationship with D explained 85 % of variation in E (Figure 7.4). Thus despite apparent decoupling transpiration was strongly correlated with D. This highlights one of the problems of treating the canopy as a single layer, that sinks for

energy and sources of water are assumed evenly distributed throughout the canopy (Jarvis et al. 1981, Denmead 1984). If coupling is strongest where most radiation is absorbed then control of transpiration may be largely by vapour pressure deficit even if Ω is quite large. Theoretically at the high values of Ω observed, E should have approached the equilibrium rate (E_{eq}) resulting from the continued input of radiation and consequent increase in the sensible and latent heat content of the boundary layer (Jarvis 1985). In practice E_{eq} was given a large weighting by Ω when E was poorly correlated with R_n and under strong diffusive control (Figure 7.4). In addition E was high when low values of R_n were observed, resulting in underestimation of E by E_Ω at higher rates. Under well watered conditions, and when evaporative demand was moderate, boundary layer conductance was not large enough in relation to stomatal conductance in this canopy to be ignored. The high r^2 value for the linear relationship which expressed g_a as a function of u and h (Table 7.3) may have some utility.

As discussed in chapter 5 one solution to the problem of differential distribution of sources and sinks of and for heat and water vapour is to divide the canopy into layers. The Penman-Monteith equation is applied in one of its forms to each of the layers and the results summed to give an estimate of canopy transpiration. Examination of the vertical profile of g_s, g_a, Ω, E_{imp} and E_Ω indicated that this approach was appropriate in this study. Overestimation of E by E_{imp} and E_m increased with depth in the canopy. This was largely the result of decreasing g_a which resulted in an increase in the difference between D_s and D with depth (Table 7.6). Calculation of transpiration as E_Ω markedly improved prediction of E, relative to E_{imp} and E_m, for all three canopy layers (Figure 7.5). While E_Ω was a very good predictor of E in all canopy layers it did overestimate E increasingly with canopy depth (Figure 7.5). Net radiation was attenuated by the Beer-Lambert Law assuming an extinction coefficient of 0.5. This value is at the upper end of those considered appropriate for plants with hanging foliage (Saeki 1960, Chang 1968). Roberts and Rosier (1992) also used 0.5 for *E. camaldulensis* while Dye (1987) used 0.4 for *E. grandis*. Attempts to define extinction coefficients for tree crops have largely been restricted to conifers (Jarvis et al. 1976, Smith et al. 1991). The

observation that E_{Ω} overestimated E in the lower canopy where average Ω was 0.84 suggests that a higher extinction coefficient might be more appropriate for *E. globulus*.

Mean Ω for the upper, middle and lower layer was 0.29, 0.40 and 0.84 respectively. The mean value of Ω for the upper canopy layer was still quite high, although lower than values reported for the same layer of *A. excelsium* (Meinzer et al. 1993). On the other hand Ω was higher in the lower third of the irrigated *E. globulus* tree than was reported for the lower crown of *A. excelsium* (Meinzer et al. 1993). While Ω increased with depth the radiation load decreased significantly. On average 64, 33 and 3 % of R_n respectively was absorbed by the upper, middle and lower layer of the canopy. The observation that high values for Ω at the canopy scale were not associated with strong control of transpiration by radiation is partially accounted for by this result and suggests that the best coupled portions of the canopy were those where most radiation was absorbed. Similarly the decoupled portion of the canopy received a very low radiation load. Moreover, when E was expressed as a function of R_n for each layer, the fit improved with canopy depth while the reverse was true for E expressed as a function of D (Figure 7.6).

The single layer model for predicting E (E′) is attractive because it only requires estimation of stomatal conductance for upper canopy foliage (g_{su}). Moreover the scheme used here (Raupach 1995) to estimate canopy conductance gave greatest weighting to well lit upper canopy foliage and was consistent with the concept of a 'maximum surface conductance' (McNaughton 1994, Kelliher et al. 1995). Application of this big leaf model assumes perfect coupling but could nevertheless be used satisfactorily to predict transpiration (E′) in a canopy of high L* which was not perfectly coupled. In well coupled canopies (for example those of lower L*) this model and the multi layer model converge so that canopy conductance calculated from equation (6.9) may be used in equation (7.8) or (7.9), both of which assume perfect coupling, to estimate the transpiration rate of irrigated and rainfed canopies of both *E. globulus* and *E. nitens*. If transpiration may be estimated for both coupled and decoupled canopies by using Raupach's integration

scheme and an assumption of perfect coupling then it follows that any stomatal response to water stress will reduce water use efficiency at the canopy scale. This will probably mean that both the growth rate and water use efficiency of biomass production will be more affected by water stress in *E. nitens* than *E. globulus*. This is an issue which will be considered further in the following concluding chapter.

Chapter 8. A review of drought responses of *E. globulus* and *E. nitens* and a consideration of their implications

8.1 Introduction

This thesis has considered some physiological responses to drought of *E. globulus* and *E. nitens*. Interspecific differences were also described, together with some underlying seasonal and diurnal patterns. The data presented were measured in a plantation in which the two species were grown side by side under irrigated and rainfed conditions. The overall aim was to describe physiological strategies adopted by *E. globulus* and *E. nitens* in their response to water stress with a view to assessing their suitability for establishment on water limited sites. In the opening chapter a water limited site was defined as one where potential evaporation exceeded rainfall. This is a useful working definition as on such sites plantation growth will either be water limited or unsustainable in the long term if reliant on stored water.

On sites where growth rates are likely to be high enough to justify establishment of either of these fast growing species, water limitation, under the definition proposed above, will occur during the summer and in a pattern similar to that imposed in the current study. That is, water stress will occur in a series of distinct cycles. With this premise in mind this chapter summarises the physiological responses of *E. globulus* and *E. nitens* to water stress, together with interspecific differences which were independent of water stress, and discusses these in terms of their implications for the growth and water use efficiency of the two species, and hence their suitability for establishment on sites where moderate water stress is the only limitation to growth.

8.2 Summary of results

8.2.1 Leaf water relations (chapter 3)

In early spring of 1991 and 1992 osmotic potential (at full turgor and turgor loss point) in the irrigated *E. nitens* was significantly lower than at other times of the year (Figure 3.2a and 3.2b). Water stress reduced osmotic potential and increased bulk elastic modulus in *E. nitens* while the reverse occurred in *E. globulus*. Treatment effects on osmotic and elastic properties were overshadowed by interspecific differences. These were most apparent in April 1993, at the end of the sixth period of water stress, when the osmotic potential at full and zero turgor were significantly higher and bulk elastic modulus significantly lower in *E. globulus* than *E. nitens*. The combination of these interspecific differences in leaf osmotic and elastic properties resulted in the slope of desorption isotherms being significantly higher in the region of positive turgor for *E. nitens* than *E. globulus* (Figure 3.3i). This was manifested as turgor loss at significantly higher leaf relative water contents in *E. nitens* (0.87) than *E. globulus* (0.79), an interspecific difference which was independent of instantaneous or cumulative water stress.

8.2.2 Leaf area development (chapter 4)

Allometric relationships between leaf area and sapwood area were developed by destructive sampling in July 1992 and July 1993 (Figure 4.1 and 4.2). The mean slope (across species and treatments) of relationships between leaf area and sapwood area at 1.3 m above ground was significantly lower in July 1993 (0.57) than July 1992 (1.06). In 1992 species rather than treatment determined the slope and y-intercept of the relationships and the effect of species on the slope of the relationships was almost significant ($p=0.062$). In contrast to 1992, the slope was decreased appreciably by irrigation ($p=0.12$) in 1993 from 0.70 to 0.48 in *E. globulus* and 0.61 to 0.47 in *E. nitens* (Table 4.3). The effect of species on the slope had become less important than in 1992 ($p=0.45$).

These allometric relationships were used with monthly growth data to plot the course of leaf area index (L*) between August 1991 and April 1993 (Figure 4.3).

L* was significantly lower in *E. nitens* than *E. globulus* throughout the study and was significantly reduced by water stress after November 1992. During the 1992/93 growing season the L* of the rainfed *E. globulus* increased rapidly after rewatering, resulting in a stepped pattern of leaf area development which was not observed in *E. nitens*. At the end of the experiment, in April 1993, L* of the irrigated and rainfed treatments were, respectively 8.3 and 6.1 in *E. globulus* and 6.9 and 4.3 in *E. nitens*.

8.2.3 Stomatal conductance (chapters 5 and 6)

E. globulus and *E. nitens* both exhibit stomatal control of transpiration as their principal response to drought. Daily maximum g_s of both *E. globulus* and *E. nitens* was significantly reduced when ψ_{max} was <-0.55 MPa. Reduction in g_s as ψ_{max} decreased was greater in *E. nitens* than *E. globulus*. After rewatering g_s was slower to recover in *E. nitens* than *E. globulus*. These differences caused a significant species by water stress interaction. A phenomenological model of stomatal conductance of upper canopy foliage (g_{su}) was developed for the irrigated trees. The maximum g_{su} observed (387 mmol m^{-2} s^{-1}) was attenuated with normalised functions of total solar radiation (Q), air temperature (T) and vapour pressure deficit (D). This model explained 70% of the variation in g_{su}. The effect of water stress on the daily total of g_{su} was accommodated by predicting the ratio of total daily stomatal conductance of rainfed to that of irrigated trees as a function of the cumulative water stress integral for the preceding x days ($S_{\psi x}$), where x was eight days for *E. globulus* and 20 days for *E. nitens*. Using $S_{\psi x}$ as an independent variable accommodated the longer residual effect of water stress in *E. nitens* than *E. globulus*. The model explained 75 and 73% of the residual variation in the daily total of g_{su} of *E. nitens* and *E. globulus* respectively after the direct effects of Q, T and D were removed.

8.2.4 Canopy conductance and regulation of transpiration (chapters 5 and 7)

Two estimates of canopy conductance were compared in the irrigated treatment of both species. The first (g_c) was a summation of the conductances of three canopy layers and the second (g_c') involved integration of the light response function of the

leaf level model with respect to cumulative leaf area index. At a daily time step g_c' explained 85% of the variation in g_c when L* was less than 6, but underestimated g_c by as much as 41% at leaf area indices above 6. This underestimation indicated that at high L*, *E. globulus* and *E. nitens* canopies may be weakly coupled to ambient atmospheric conditions. The degree of coupling was investigated in the irrigated *E. globulus* by simultaneous measurement of transpiration (using sapflow sensors) and stomatal conductance over three days in March 1994. The mean value of the dimensionless decoupling coefficient (Ω) was 0.63. Despite this a linear relationship with D explained 86% of the variation in transpiration. The vertical profile of Ω and absorbed net radiation were examined and Ω was greatest where the smallest amount of radiant energy was absorbed.

8.3 Implications of observed responses

8.3.1 Growth

Lower osmotic potentials in leaves have been associated with a capacity for water uptake from drier soil and the maintenance of higher relative water contents at a given leaf water potential (Morgan 1984, Pereira and Pallardy 1989). The maintenance of higher relative water contents in *E. nitens* was not associated with turgor maintenance. *E. nitens* maintained higher relative water contents than *E. globulus* at any given water potential but *E. nitens* lost turgor at a higher relative water contents than *E. globulus*.

Maintenance of positive turgor is essential for but not uniquely related to leaf expansive growth. The presence of sufficient turgor must be combined with adequate cell wall extensibility (Bradford and Hsiao 1982, Boyer 1985, Cosgrove 1987). Notwithstanding this qualification, the maintenance of positive turgor down to significantly lower relative water contents in *E. globulus* than in *E. nitens* will probably be associated with greater rates of leaf initiation and expansion in *E. globulus* than *E. nitens* during periods of moderate water stress. This is consistent with the observation that the development of leaf area index was more reduced by water stress in *E. nitens* than *E. globulus*.

While it is clear that stomatal closure will restrict the diffusion of CO_2 into the sub-stomatal cavity thereby reducing the rate of photosynthesis, the relative importance of stomatal and non-stomatal limitations to carbon assimilation during drought remains unclear. Two theories persist: that reduction of photosynthesis during water stress occurs exclusively in the gaseous phase (Kaiser 1987) or that this reduction is due to a combination of stomatal and mesophyll limitation (Wong et al. 1985c, Eastman and Camm 1995). At the leaf level stomatal conductance (g_s) was more rapidly reduced by water stress in *E. nitens* than *E. globulus*. Similarly g_s was slower to recover after rewatering or rainfall in *E. nitens* than *E. globulus*. It is therefore reasonable to suggest that the rate of photosynthesis per unit leaf area will be more reduced by water stress in *E. nitens* than *E. globulus*. The maximum rate of photosynthesis was consistently greater for *E. nitens* ($\approx$20 μmol m^{-2} s^{-2}) than *E. globulus* ($\approx$15 μmol m^{-2} s^{-1}) which will tend to offset the greater stomatal limitation to water stress in the former species (Battaglia et al. 1996).

Total biomass production for a given soil water status will be proportional to intercepted radiation (Linder 1985) which will in turn be proportional to leaf area index, L* (Landsberg 1986). The greater reduction in L* during periods of water stress, in absolute and relative terms, in *E. nitens* than *E. globulus* will compound any leaf level effect on the rate of photosynthesis mediated by stomatal closure. If the optimisation principle holds (Bierhuizen and Slatyer 1965, Cowan and Farquhar 1977) the rate of photosynthesis will be distributed throughout the canopy in a way that is correlated with the distribution of measured g_s. If this is true then canopy photosynthesis will be closely correlated to canopy conductance calculated as the sum of the conductances of individual canopy layers (g_c).

The extent to which the greater effect of water stress on calculated canopy conductance, and by analogy photosynthesis, in *E. nitens* than *E. globulus* is manifested as a reduction in wood production will depend on the effect of water stress on biomass partitioning. While this was not investigated, growth data were collected throughout the course of the experiment. The standing volume of wood,

calculated after Opie (1976), was significantly less in *E. nitens* than *E. globulus* after October 1992, but was only significantly affected by water stress after March 1993. From this time the difference in standing volume between the species was greater in the rainfed than the irrigated treatment but no significant species by water stress interaction was observed. In the fourth year of growth the volume increment of the irrigated and rainfed treatments were, respectively 44.8 and 23.9 m^3 *E. globulus* and 41.4 and 17.8 m^3 in *E. nitens* (Honeysett et al., unpublished data). These increments are consistent with the greater effect of water stress on leaf area index and stomatal conductance in *E. nitens* compared to *E. globulus*.

8.3.2 Transpiration

It has been argued that due to their aerodynamic properties forests are strongly coupled to the atmosphere so that changes in transpiration (E) are regulated by and stomatal aperture and D (Jarvis and McNaughton 1986). However, results presented in chapter 5 and 7 show that at leaf area indices >6 *E. globulus* or *E. nitens* plantations may be weakly coupled to atmospheric conditions. The difference between canopy conductance calculated as the sum of the conductance of individual canopy layers (g_c) and that calculated by integration of f(Q) with respect to cumulative leaf area index (g_c') is indirect evidence of decoupling. The significant overestimation of measured E if calculated from g_c and vapour pressure deficit (D) assuming perfect coupling is direct evidence that at high L*, *E. nitens* and *E. globulus* plantations can be weakly coupled to ambient atmospheric conditions.

Given that the canopies of irrigated trees of *E. globulus* and *E. nitens* were weakly coupled to the atmosphere, it is inappropriate to use g_c to calculate transpiration in a single layer formulation of the Penman-Monteith equation (Monteith 1965). The integration scheme proposed by (Raupach 1995) and used to calculate g_c', weights foliage according to the amount of radiation received. This approach attenuates the contribution of foliage from the top to the bottom of the canopy as an exponential decay function of cumulative leaf area index, and is appropriate for high L* plantations given the observation in chapter 7 that the decoupling coefficient (Ω) increased from the upper to the lower canopy layer. Transpiration calculated as a

function of g_c' and D (Tan and Black 1976, Tan et al. 1978, Dye and Olbrich 1993) closely approximated E measured using sapflow sensors. Given that g_c and g_c' converge as L* decreases, it follows that E may be calculated using g_c' and D in equation 7.9 (Tan and Black 1976) for *E. globulus* and *E. nitens* plantations at any leaf area index.

The L* of the irrigated treatment was greater than 6 after canopy closure in both *E. globulus* and *E. nitens*. Above this value predicted g_c' was a very weak function of L* so that under irrigated conditions *E. globulus* and *E. nitens* might be expected to transpire at much the same rate. Total evapotranspiration, calculated fortnightly by soil water balance, for the year from July 1993 to June 1994 was 1550 and 1554 mm for the irrigated *E. globulus* and *E. nitens* respectively (Table 8.1). The predicted effect of water stress on total daily g_c' was greater for *E. nitens* than *E. globulus* so that the effect of water stress on E will also be greater in *E. nitens* than *E. globulus*. Predicting the effect of water stress on transpiration as a function of g_c' calculated with equation 6.9 combines the effect of water stress on L* and g_s. The effect of water stress on transpiration calculated using g_c' in equation 7.9 is less than would have been predicted using the same equation and g_c.

8.3.3 Water use efficiency of growth

If transpiration is directly proportional to g_c' and assimilation is directly proportional to g_c then as L* increases above about 5.5 water use efficiency will increase. The corollary of this is that any effect of water stress on L* will tend to reduce the water use efficiency of canopy photosynthesis in the long term. Combining this with the reduction of g_s during water stress will further reduce water use efficiency in the short term. Given that water stress more strongly reduced g_s and L* of *E. nitens* compared to *E. globulus* it may be inferred that growth and water use efficiency will be more affected by water stress in *E. nitens* than in *E. globulus*.

The ratio of annual volume growth to annual water use is the measure of water use efficiency most relevant to forest managers. If this is expressed as a reciprocal the amount of water required to produce a unit of stem volume is estimated. A decrease in this ratio with time will occur during plantation development due to an increase in partitioning to stems (Beadle and Inions 1990) but the values were always less in *E. globulus* than *E. nitens* in both treatments and the differences between the species were larger in the rainfed than the irrigated treatment (Honeysett et al, unpublished data). When this ratio was calculated for the period from July 1993 to June 1994 the value for the rainfed *E. globulus* (40 mm m^{-3}) was only slightly greater than for the irrigated treatment. In contrast water stress increased this ratio from 37 to 53 mm m^{-3} in *E. nitens* (Table 8.1, Honeysett et al. unpublished data). This is consistent with the observed effects of water stress on g_c and g_c in the two species and confirms that when the effect of water stress on leaf area index and stomatal conductance are combined, a greater reduction in growth and water use efficiency will occur in *E. nitens* than *E. globulus*.

Table 8.1 The increase in stem volume (CAI), total evapotranspiration (E_t) and the amount of water transpired for each m^3 of wood produced between July 1993 and June 1994, by species and treatment. Evapotranspiration was calculated by soil water balance after (Honeysett et al. 1992) and CAI was calculated as the difference between standing volume of timber in July 1993 and June 1994 after Opie (1976).

	CAI (m^3)	E_t (mm)	WUE^{-1} (mm m^{-3})
E. globulus (I)	44.8	1550	35
E. nitens (I)	41.4	1554	37
E. globulus (R)	23.9	950	40
E. nitens (R)	17.8	950	53

8.4 Species selection for establishment on water limited sites: a concluding comment

The original hypothesis advanced was that *E. nitens* would be more tolerant of drought than *E. globulus* by virtue of a higher concentration of osmotica associated with its cold tolerance (Hallam et al. 1989). The results presented in this thesis have disproved this null hypothesis. While *E. nitens* does maintain a lower osmotic potential than *E. globulus*, neither species demonstrated a capacity to adjust osmotically in response to water stress. The combination of a lower osmotic potential and higher bulk elastic modulus in *E. nitens* than *E. globulus* resulted in turgor loss at a higher leaf relative water content in *E. nitens* than in *E. globulus*. Moreover these differences in leaf water relations were associated with a greater reduction of stomatal conductance, leaf area index and canopy conductance during water stress in *E. nitens* than *E. globulus*, and in the long term reduced the volume growth and water use efficiency of wood production more in *E. nitens* than in *E. globulus* (Honeysett et al. unpublished data).

This study compared the responses of these two species to cyclical moderate water stress. It is clear that under these conditions *E. globulus* produces more wood with greater water use efficiency than *E. nitens* and should be the species of choice where available water is the only factor limiting growth. The experience of the 1993/94 drought in Western Australia provides a cautionary footnote to this finding. During this prolonged drought some 600 ha of *E. globulus* plantations died due to water stress (Dutkowski 1995). This demonstrates that the turgor maintenance strategy of *E. globulus* leaves it vulnerable to prolonged soil water deficit in environments where evaporative demand is high, as is the case in SW Western Australia. The more conservative response of *E. nitens* is unlikely to result in it surviving severe drought for a significantly longer time than *E. globulus*. *E. globulus* and *E. nitens* exhibit rapid early development of leaf area. This large leaf area intercepts the radiation which drives their rapid growth under favourable conditions but without the capacity to shed foliage both species are vulnerable to

the sort of catastrophic cavitation described by Tyree and Sperry (1988). While *E. globulus* grows more quickly during and after moderate water stress than *E. nitens*, neither species appears well adapted to severe water stress. If plantation establishment is to continue on sites where extended periods of water stress are anticipated then the slower growth rates which attend drought tolerance must be accepted and consideration given to species with slower inherent growth rates.

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